

# *THE* **INSECTS** *OF* **AUSTRALIA**

A textbook for students and research workers

**Second Edition**

**VOLUME II**



Division of Entomology **CSIRO** Australia



Insects are among the most diverse and durable forms of life. In Australia alone there are over 85 000 species—overwhelmingly more than all of the vertebrate species in the entire world. Insects exhibit apparently endless variety in appearance and biology and their many peculiarities are responses to millions of years of environmental challenge and change. Insects are significant and often dominant organisms in almost all terrestrial and freshwater habitats; they are of immense importance to the stability of the environment and to human welfare.

These two volumes provide a comprehensive account of Australia's distinctive and exciting insect fauna. The volumes include detailed treatments of the morphology and biology of all insect orders and up-to-date summaries for all families known to occur in Australia. Keys using structural features, over 2000 black-and-white illustrations, colour plates and electron micrographs enable the reader to place any Australian insect in its correct family. Also featured is a unique and invaluable key to orders.

While the format of the first (1970) edition of *The Insects of Australia* has been retained in these two volumes, knowledge about Australian insects has increased enormously since 1970. All chapters have been entirely rewritten and substantially expanded, and three new chapters have been included. This new edition is the work of more than 70 experts from around the world.

Jacket illustrations: *front*: *Lychnocolax* sp., male (Strepsiptera: Myrmecolacidae) [K. Pickerd]; *spine*: *Phalacrognathus muelleri* (Macleay), king stag beetle (Coleoptera: Lucanidae) [J. Green]; *back*: *Chenuala heliaspis* (Meyrick), anthelid caterpillar (Lepidoptera: Anthelidae) [B. Jessop]; *Stethomela* sp., leaf beetle (Coleoptera: Chrysomelidae) [C. D. and D. W. Frith]; limacodid caterpillar (Lepidoptera: Limacodidae) [D. C. F. Rentz]; *Anthela guenei* (Newman), anthelid moth (Lepidoptera: Anthelidae) [B. Jessop]











Donat Agosti

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Zürich

**The  
Insects of  
Australia**







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*A textbook for students  
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DIVISION OF ENTOMOLOGY  
COMMONWEALTH SCIENTIFIC AND  
INDUSTRIAL RESEARCH ORGANISATION



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# Coleoptera

(Beetles)

J. F. LAWRENCE and E. B. BRITTON

Endopterygote Neoptera, with mesothoracic wings modified into more or less hardened, non-folded, rigid elytra, which usually meet edge to edge in a straight line when at rest and partly or wholly cover the hind wings and abdomen; metathoracic wings, when developed, membranous, folded, and alone used for propulsion in flight; mouth-parts almost always mandibulate (rarely suctorial or reduced); prothorax well developed, almost always free, and forming with the head a distinct fore body, contrasting with hind body, which consists of mesothorax, metathorax and abdomen; body usually more or less depressed, so that coxae and pleural regions lie ventrally; fore coxae variable in shape and usually recessed into cavities formed by the sternum and notum (Polyphaga) or sternum and pleura; mesothorax usually reduced; mid coxae usually globular and more or less recessed into cavities formed by the meso- and metasterna and usually the mesopleura; mesoscutellum usually visible from above between elytral bases; metasternum usually well developed, with single endosternite originating at or near its posterior edge; hind coxae usually transverse, often less deeply recessed and sometimes with posterior excavations which receive the femora; abdominal sternites almost always more heavily sclerotised than tergites, the basal one or two usually reduced and concealed beneath the hind coxae; terminalia usually telescoped into apex of abdomen. Larva with or without thoracic legs; with a distinct head capsule, antennae and mandibulate mouth-parts (rarely suctorial, entognathous or reduced); very rarely with abdominal prolegs. Pupa aedeicous and exarate or rarely obtect.

There are more than 300 000 named species of Coleoptera in the world. About 40% of all insects and 30% of all animals are beetles; the number of beetle species exceeds that of fungi or of vascular plants and is more than 6 times that of vertebrates. There have been about 20 000 species described from Australia, but several thousand more are known in collections and the true number may exceed 30 000. Curculionidae is the largest family, with more than 6000 Australian species. Scarabaeidae and Chrysomelidae each has about half that number, Carabidae about 2500, and Staphylinidae, Tenebrionidae and Cerambycidae each between 1200 and 1500 species.

It is generally conceded that the single most important factor contributing to the success of Coleoptera is the development of sclerotised fore wings or elytra, resulting

in the protection of the folded hind wings when not in use and permitting the occupation of enclosed spaces and cryptic habitats by adults. This was accompanied by a series of other morphological changes, including the flattening of the body, the recession of fore and mid coxae into cavities, and the general reduction of exposed membrane, all of which contributed to increased survival in cryptic habitats by protecting the body from both predation and infection by micro-organisms. Another important result of elytral development was the formation of a series of interlocking devices joining the elytra, prothorax and abdomen, so that an enclosed space, the *sub-elytral cavity*, was formed beneath the elytra, enclosing the metathoracic and abdominal spiracles and reducing water loss through transpiration (Cloudsley-Thompson 1965).

Although the order must have originated in the warm, humid environments of the Carboniferous, the first significant radiation of beetles apparently took place in more xeric and temperate environments, as represented by Permian fossils from the Ural Mountains and Siberia. Reviews of the Mesozoic history of beetles may be found in Arnoldi *et al.* (1977), Crowson (1975) and Ponomarenko (1969b, 1986).

Beetles are generally thought to be most closely related to the neuropteroid complex but not to any single order within that group. The position of the Strepsiptera is questionable, but they are usually considered to be the sister group of Coleoptera on the basis of hind wing dominance, free prothorax, heavily sclerotised abdominal sternites and furcate metendosternite. Similarities based on the 1st instar larvae are certainly homoplasious (pp. 100, 136, 178, 690).

The most recent textbook dealing exclusively with Coleoptera is that of Crowson (1981), which covers in detail most aspects of beetle biology. Basic references on beetle classification include those of Crowson (1955, 1960, 1967) and Lawrence and Newton (1982). Lawrence (1982) gives brief descriptions of families and higher taxa based on both adults and larvae. The Australian fauna has been treated by Britton (1970), and regional manuals on Australian beetles are being produced by E. G. Matthews (1980–87) for South Australia and Moore (1980–89) for south-eastern Australia. Hawkeswood (1987a) includes colour photographs and popular accounts of 176 species.

#### Anatomy of Adult

**Head.** The head (Fig. 35.1A) is a rigid capsule, which is primitively *prognathous*, with the mouth-parts facing forward; this orientation is assumed in the descriptive sections below, although the *hypognathous* condition, with ventrally oriented mouth-parts, occurs in a number of beetle groups. The head may be divided into fairly well-defined areas, useful for descriptive purposes but of little significance for purposes of homology (p. 114). The frons (or front) is that part of the upper surface lying between the eyes and limited anteriorly by the clypeus (or epistoma), which is usually separated from the frons by a frontoclypeal (or epistomal) suture, ridge or declivity. The frons may be further subdivided, the area behind the eyes being called the *vertex* and the posterior edge of the head adjacent to the occipital foramen the *occiput*. In some hypognathous forms, there is a *transverse occipital ridge* (Fig. 35.15F), which fits against the anterior edge of the pronotum. Those portions of the head capsule below the eyes on each side are called the *genae*, and these extend mesally to meet the *gular sutures*, which define a ventral region called the *gula* (Fig. 35.1B); in some forms the sutures may be fused or absent, so that the genae extend to the midline.

The compound eyes are highly varied in size and may be absent or so large that they meet above and/or below the head. In a number of families the eyes are anteriorly emarginate or partly divided by a lobe (*canthus*), and in Gyrinidae, some Scarabaeoidea and a few other groups the division into an upper and lower portion may be com-

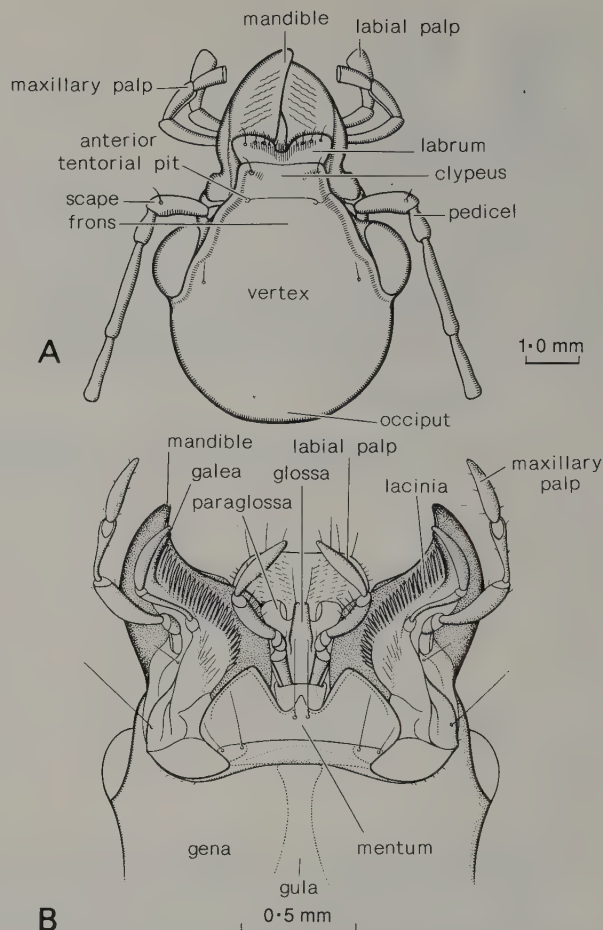


Fig. 35.1 Head: A, *Calosoma schayeri*, Carabidae, dorsal; B, *Hypharpax* sp., Carabidae, ventral. [F. Nanninga]

plete. The facets of the eye tend to be small and flat in diurnal species and coarse and convex in those forms active in reduced light. The structure of the ommatidium (p. 49), which has been surveyed by Caveney (1986) for most families of beetles, has proven useful in characterising major groups, such as the Cucujiformia (p. 644). A *eucone* eye, possessing a crystalline lens, is considered to be primitive in Coleoptera; derived eye types include *acone*, in which the crystalline lens has been lost, and *exocone*, in which a lens is formed from the cornea. A median ocellus occurs on the frons in most Dermestidae and one staphylinid (*Metopsia*), and there are 2 ocelli present in *Ragyodes* (Leiodidae), omaliine Staphylinidae and Derodontidae. The presence of 3 ocelli has been observed only in teratological specimens of a few omaliine Staphylinidae (Naomi 1987; Newton and Thayer unpubl.).

The antennae are normally 11-segmented with a clearly differentiated scape and pedicel, but reductions to 10, 9 or 8 segments are relatively common; a few groups (e.g. some Pselaphidae, Hydrophilidae, Scarabaeidae, Coccinellidae) may have 7 or fewer, and males of Rhipiceridae may have more than 30. The length of the antenna varies considerably and may be much longer than the body in some Cerambycidae and Anthribidae. Antennal



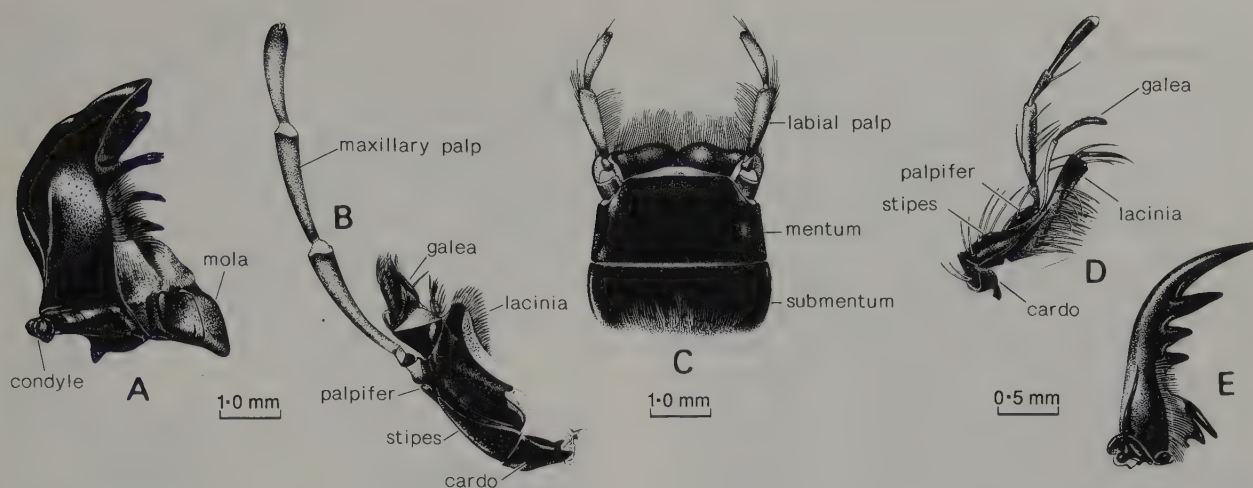


Fig. 35.2 Mouth-parts. *Hydrophilus latipalpus*, Hydrophilidae: A, mandible, ventral; B, maxilla, ventral; C, labium, ventral. *Cicindela semicincta*, Carabidae: D, maxilla, ventral; E, mandible, ventral. [F. Nanninga]

form is equally varied and is often used as a diagnostic feature. The antennae may be *filiform* (slender and linear, Figs 35.3A, 21F–H), *moniliform* (like a string of beads, Figs 35.21A, 47D), *incrassate* (gradually enlarged apically, Figs 35.25G, 28A, 50C, D), *geniculate* (elbowed between the elongate scape and the rest of the antenna, Fig. 35.62J), *serrate* (saw-like, Figs 35.34, 36E, 38E, F), *pectinate* (comb-like, Figs 35.37B, 38A), *flabellate* (extreme development of pectinate type, Figs 35.35, 37A), *clavate* or *capitate* (distinctly clubbed, Figs 35.44B, C, F, 47F–I, 48), or *lamellate* (with an asymmetrical club of more or less flattened segments, Figs 35.29A, E, F). Antennae are frequently longer (e.g. Cerambycidae) or more elaborate (e.g. Callirhipidae, Figs 35.37A, B) in the male than in the female. The antennae are primarily chemosensory organs and the apical segments bear a variety of sensilla; in aquatic Hydrophilidae, modified antennae (Figs 35.23E–G) are utilised in respiration by breaking the surface tension and allowing air to enter the bubble trapped beneath the body by a plastron (pp. 41, 42, 560). Modified antennae in the males of some beetles may be used in courtship (e.g. in Melyridae, Meloidae) or possibly in male combat (e.g. in Laemophloeidae, Pterogeniidae).

The labrum is usually a transverse flap, clearly visible from above and attached to the clypeus by membrane; in some beetles, however, it may be membranous and concealed beneath the clypeus, as in some Scarabaeidae, or solidly fused to the clypeus, as in Curculionidae. The area lying beneath the labrum and clypeus and forming the upper wall of the preoral cavity is called the *epipharynx*. A pair of sclerites, the *tormae*, often lie in the basolateral angles of the labrum and extend on to the epipharyngeal surface of the clypeus.

The mandible (Figs 35.2A, E) is basically in the form of a tetrahedron, with dorsal, ventral and external faces, a triangular base, and articulations with the head capsule consisting of a dorsolateral socket and ventrolateral condyle. Mandibles move in a transverse plane, through the action of a large adductor and smaller abductor mus-

cle, and the apices are opposable; in some Corylophidae, however, the stylet-like mandibular apex is separated by membrane from the base, and the same muscles produce a forward-backward movement. The basal portion of the mandible's internal (mesal) edge, when thickened, enlarged and usually armed with ridges or tubercles, is called the *mola*; the two molae act together to grind or otherwise process food, and they are absent in most predacious forms. The mandibular apex is variously armed with teeth, and between it and the molar region, there may be a tooth-like *retinaculum* and/or a membranous *prostheca*. Mandibles attain their maximum development in males of some Lucanidae, where they are used solely in combat with other males; by contrast some Scarabaeidae have the mandibular apex reduced and more or less membranous.

The maxilla (Figs 35.2B, D) consists of a basal *cardo* and an apical *stipes*, to which are attached a *palpifer* bearing the 3- to 5-segmented palp, an external (lateral) *galea* and an internal (mesal) *lacinia*; the galea may be 1- or 2-segmented and the lacinia is 1-segmented but may be reduced or absent.

The labium is attached at the anterior end of the gula (or genae when the gula is absent) and usually consists of a basal *mentum*, an apical *prementum*, and paired *palpifers*, to which the 1- to 3-segmented palps are articulated. The apex of the prementum, known as the *ligula*, is sometimes divided into two or more lobes probably homologous with the *glossae* and *paraglossae* of primitive insects (p. 8). In some forms, including *Hydrophilus* (Fig. 35.2C), a distinct sclerite, the *submentum*, lies between the gula and mentum, but the term has also been applied to the undifferentiated anterior portion of the gular region.

The tentorium consists of a transverse connecting piece or bridge joining a broad pair of posterior arms, which terminate at the posterior tentorial pits located along the gular sutures, a narrower pair of anterior arms which extend forward and terminate at the anterior tentorial pits, which are often located along the frontoclypeal suture,

and sometimes a third pair of dorsal arms, which terminate on the roof of the head capsule. The details of tentorial structure vary considerably (Stickney 1923) and may provide useful taxonomic characters. In many members of the Polyphaga a pair of *cervical sclerites* lies in the membrane between the head and prothorax.

**Thorax.** The *prothorax* in Coleoptera is always well developed, forming with the head an obvious fore body separated by intersegmental membrane from the hind body, which consists of the mesothorax, metathorax and abdomen.\* The prothorax is composed of a large dorsal sclerite, the *pronotum*, which extends ventrally on each side to meet the lateral pleura (except in Polyphaga, see below), and a ventral sternum, which lies in front of and forms the anterior and mesal walls of the *coxal cavities*. The details of prothoracic morphology and evolution are complex and have been discussed by Baehr (1979b), M. E. G. Evans (1971, 1974), Hlavac (1973, 1975) and Larsén (1966).

In Archostemata, Myxophaga and Adephaga, the pleuron on each side is visible externally, forming part of the thoracic wall and separated from the notum and sternum, respectively, by *notopleural* and *pleurosternal* sutures (Figs 35.3A, B); it may be divided into an anterior *proepisternum*, forming the major part of the wall, and a posterior *proepimeron*, which may extend mesally to meet the sternum, closing the coxal cavity from behind. The pleurosternal sutures are occasionally absent, as in *Omma* and *Tricondyla*. The deflexed portion of the pronotum, which lies adjacent to the episternum, is called the *pronotal epipleuron*, and it is usually separated from the upper portion or *disc* by a carina (often referred to as the lateral 'margin' or 'edge' of the pronotum). The *trochantin* is a small sclerite articulating by a single condyle with the coxa but separated by membrane from the pleuron; the coxa also articulates directly with the pleuron.

In Polyphaga (Figs 35.3C, 15I–S), the prothoracic pleuron has become reduced and internalised, so that it is represented only by an *endopleuron*, which is fused to the trochantin and not visible externally; the notopleural suture is absent, the coxa articulates with the trochantin at two points, and the deflexed portion of the notum, called the *hypomerion*, is attached directly to the sternum and separated from it by a *notosternal suture*. In some Polyphaga, the trochantin may be reduced, concealed, and/or fused to the notal wall, and in others the notosternal suture may be absent. The anterior portion of the sternum varies considerably among Polyphaga, being highly reduced in Eucinetoidae and some Staphylinoidae, well developed in many groups, and produced forward forming a chin piece and concealing the mouth-parts in some members of Histeridae, Elateridae and a few other families.

The meso- and metathorax are immovably fused together to form the *pterothorax*, which bears the elytra and wings (Figs 35.3, 6, 12). The mesothorax is reduced

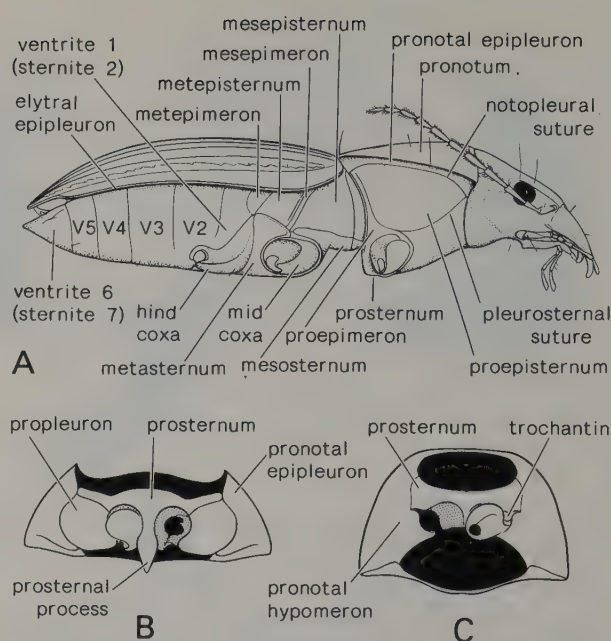


Fig. 35.3 A, *Notonomus violaceus*, Carabidae, lateral. Prothorax, ventral; B, *Hyderodes schuckardi*, Dytiscidae; C, *Dermestes maculatus*, Dermestidae. [A by F. Nanninga; B–C by S. Smith]

by comparison with the metathorax, except in permanently flightless forms. The dorsal surface of each of the two segments is divided into an anterior *prescutum*, a median *scutellum* and lateral *scuta* (the divided *scutum*). Behind these sclerites in the metathorax is the transverse *postnotum*. The *mesoscutellum* (referred to simply as the *scutellum*) is usually triangular and visible from above between the elytral bases. The *mesothoracic spiracles* are normally concealed in the membrane between the prothorax and mesothorax.

The ventral surface of the pterothorax is composed of the two sterna, each flanked by its pleural elements, the episterna and epimera. The mesepisterna may be modified to house portions of the fore coxae, and the mesosternum sometimes bears a deep cavity which receives the prosternal process (Figs 35.15U, 36I, 62M). The mid coxae are located in cavities, which are formed anteriorly and mesally by the mesosternum, posteriorly and mesally by the metasternum, and laterally by pleural sclerites (usually the mesepimeron alone or in combination with the mesepisternum) or by the meeting of lateral portions of the meso- and metasterna; very rarely (e.g. in Archostemata and Derodontidae) they may be partly closed by the metepisterna. The coxal cavity is said to be *laterally open* when it is partly closed by pleural elements and *laterally closed* when closed by the sterna alone.

The metasternum commonly bears a longitudinal groove and less often a transverse groove, which are usually referred to as sutures but represent invaginations associated with the metendosternite. Curved or occasionally straight lines or ridges may occur just behind the mid coxae; these are called *femoral lines* (Fig. 35.49D) and are associated with the positioning of the mid femora when at rest. The metepisterna are usually narrow and elongate,

\* In a few flightless beetles, the prothorax may be immovably fused to the hind body.



flanking the metasternum on each side, but the metepimera are reduced and usually more or less concealed beneath the elytra. The large *metathoracic spiracle* on each side is located above the mesepimeron (sometimes in a membranous pocket) and is thus concealed by the elytron. The *metendosternite* in beetles is a complex furcate structure to which several sets of muscles are attached; Crowson (1938, 1944, 1955) made extensive use of this feature as a basis for determining phylogenetic relationships among the families of Coleoptera.

**Legs.** The legs of beetles are normally adapted for walking or running, and they normally increase in size from front to rear; but in some families one or more pairs may be modified for burrowing in soil (Scarabaeidae, many Tenebrionidae), tunnelling in wood (Bostrichidae, scolytine and platypodine Curculionidae), swimming (Dytiscidae, Gyrinidae) or jumping (Eucinetidae, alticine Chrysomelidae). The form and degree of separation of the coxae provide characters of major taxonomic importance, as does the number of tarsal segments.

The fore and mid coxae are normally capable of limited circular movement; but they may be highly motile in soft-bodied, surface-grade beetles, such as Cantharidae, Lycidae and Melyridae. The fore coxae may be strongly transverse (Fig. 35.15i) to globular (Figs 35.15N, Q) or conical and projecting (Figs 35.15K, L, X), and the trochantin may be exposed and freely movable (Figs 35.15i, K, L) to concealed and immovable (Figs 35.15N, Q, P). Trochantins of the mid coxae are usually visible externally; metathoracic trochantins occur only in Archostemata. The hind coxae are usually transverse and less motile than the anterior two pairs, being articulated to the metasternum both laterally and near the midline. In Adephaga they are immovably fused to the metasternum. The posterior edge of the hind coxae may be excavated to receive the femora and distinct plates may be formed

which conceal the femoral bases; this condition is common in Adephaga and Elateriformia, and occurs in some other groups as well.

The trochanter articulates with the coxa and is usually largest in the hind leg. Its junction with the femur may be straight or slightly oblique, but in some groups (e.g. most Tenebrionoidea, Biphyllidae, Bothrideridae) it may be strongly oblique, so that there is direct contact between the femur and coxa; the latter type has been called a *heteromeroid trochanter* by Crowson (1955, 1981). Very long and narrow trochanters occur in some Lathridiidae and Pselaphidae. The femora are usually similar in shape on all three pairs of legs; the hind pair are inflated in some saltatorial species (some Scirtidae, alticine Chrysomelidae) but also in others that are not known to jump (bruchine and sagrine Chrysomelidae). The tibiae are usually more or less expanded towards the apex, where they often bear combs of spines or a pair of enlarged spines known as *tibial spurs*. The fore tibiae are often strongly expanded and toothed externally in digging or burrowing forms (e.g. Scarabaeoidea, Figs 35.29, 31).

Tarsi are normally 5-segmented, but the number is reduced to 4 in some large groups and 3 in others; in most Tenebrionoidea the hind pair of legs has 4 segments while the anterior 2 pairs have 5, and the same condition occurs in males of certain cucujoid families (e.g. Protocucujidae, Sphindidae, Rhizophagidae, Phloeostichidae, Cucujidae, Hobartiidae, Cryptophagidae). In most Chrysomeloidea and Curculionoidea, and a few members of other groups, the 4th tarsal segment is reduced and concealed at the base of the 3rd, which is lobed beneath (Figs 35.59F, G); these tarsi are known as the *pseudotetramerous* type. In a few groups, like Coccinellidae and Endomychidae, the tarsi are *pseudotrimerous*, in that they are 4-segmented with a similarly reduced 3rd segment. The basal 2 to 4 tarsal segments are often clothed beneath with *tarsal pads* composed of densely packed hairs or specialised adhesive setae. Adhesive setae occur on the fore tarsi of many male Adephaga, where they assist in copulation, and similar male setae occur on the fore and/or mid tarsi in some Staphylinoidea. In other groups (e.g. Dascillidae, Cantharidae, Cleridae, Coccinellidae, Chrysomeloidea and Curculionoidea), the adhesive setae occur in both sexes and are used in climbing (Stork 1980). The terminal tarsal segment normally bears 2 claws, which may be equal or unequal, connate or reduced to one, and of simple form, dentate, bifid or pectinate; sometimes each claw bears a membranous lobe or bristle beneath it. An *empodium* may arise between the tarsal claws (Fig. 35.15Y), but this is reduced or absent in many groups.

**Elytra.** The elytra are modified mesothoracic wings, which are characteristically rigid, fitting over the abdomen when at rest with their inner edges in contact. In most Polyphaga studied (Schneider 1975, 1978) and in Archostemata (Atkins 1958), the elytra are held out at an angle during flight and beat synchronously with the wings, thus contributing to the aerodynamic lift. In some Scarabaeidae (Scarabaeinae, Cetoniinae), however, the elytra are barely lifted during flight and exhibit very little movement; in Adephaga they are held rigidly out to the

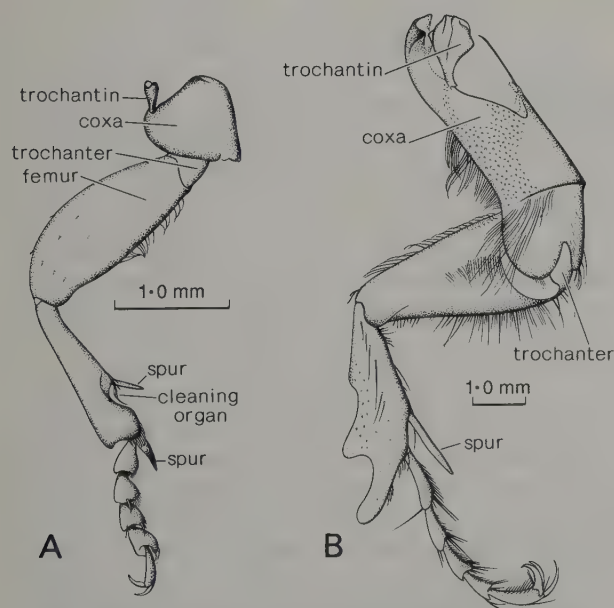


Fig. 35.4 Fore leg: A, *Hypharpax* sp., Carabidae; B, *Colpochila* sp., Scarabaeidae. [F. Nanninga]

side; and in some Silphidae they are held vertically in a roof-like position (Schneider 1975). An elytron consists of a *disc*, which is the general dorsal surface, a mesal *sutural* edge, which meets the corresponding edge of the other elytron, and usually a defined incurved lateral portion known as the *epipleuron*, which may be separated from the disc by a sharp ridge or carina; the anterolateral portion of the disc is usually somewhat elevated and angulate, forming the *humerus*, which embraces the metathoracic area shown in Fig. 35.12. The edge-to-edge fitting of the elytra at rest is often assisted by a flange on the edge of one elytron and a groove on the opposed edge; in some flightless species, however, the interlocking device may be more complex. The elytra also fit into a groove on the metanotum and may interlock with the metapleura and abdominal segments by a variety of tongue-in-groove devices or friction patches consisting of fine spicules. There is a small, 2-headed condyle at the base of each elytron, which articulates with the lateral part of the notum by means of axillary sclerites; this articular process carries blood, nerves and tracheae and acts as a point of attachment for muscles that move the elytron.

The elytral disc is usually marked by a longitudinal series of punctures, which may be contained in impressed grooves called *striae*; these *strial punctures* correspond to sclerotised pillars connecting the upper and lower surfaces of the elytron. Erwin (1974) suggested the use of *interneur* as a generic term applying to all longitudinal elytral elements, whether they be striae or puncture rows, but the term is not commonly used. The usual number of striae or puncture rows is 9 or 10, but in some groups larger numbers are present (up to 25 in some Carabidae) and in others the punctuation is confused or absent. The spaces between striae are known as *intervals*, *interstices* or *interstriae*, and these are numbered from the suture outwards and correspond to the positions of primitive wing veins, as usually indicated by the positions of nerves and tracheae in the pupa; the sutural interval is number 1, the first few intervals correspond to veins of the cubito-anal group, the lateral edge is the costal margin, and the epipleural area appears to be precostal in origin (p. 177). A short stria or puncture row, known as the *scutellary stria*, sometimes occurs adjacent to the sutural edge.

**Wings.** The metathoracic wings of Coleoptera, where functional, are nearly always longer than the elytra and at rest are folded longitudinally and transversely so that they can be concealed beneath the elytra. The wing is rotated forwards on its base into the flight position by the action of direct wing muscles; the same action spreads the wing, opening the longitudinal folds, which lead to the automatic opening of the transverse folds. In many groups of Coleoptera (Adephaga, Scarabaeoidea, Elateriformia, some Cucujiformia) a strong spring mechanism built into the wing structure keeps the wings in folded position, unless tension is provided by the direct wing muscles. In most of these no other agents are necessary to complete the folding process, but in some Scarabaeidae folding is assisted by movements of the abdomen and patches of microtrichia on the wings and abdominal terga. In some groups of beetles (Micromalthidae, Myxophaga, many

Staphylinioidea and Cucujoidea) the spring is weak or absent and the wing membrane is often long, so that folding must be assisted by movements of the abdomen, patches of spicules on the abdominal terga, and binding or friction patches on the wings and elytra (Hammond 1979; Kaufmann 1960).

Wing venation (Fig. 35.5) is somewhat reduced and modified due to the complexities of folding, making the homologisation of veins with those of other orders more difficult; in spite of this we have attempted to homologise all veins with their counterparts in other Neoptera, utilising the general venational scheme of Kukalová-Peck (1983; see Chapters 1 and 6). The nomenclature, which differs in several respects from that proposed by Forbes (1922, 1926) and followed by most coleopterists, is illustrated in Fig. 35.5 for Archostemata (A, B), Adephaga (C), Myxophaga (D, E) and Polyphaga (F, G), and the equivalent terms used by Forbes, Hamilton (1972b) and Ponomarenko (1973) are discussed below.

The main veins normally visible (at least in Archostemata, Fig. 35.5A) are: costa (C+) and subcosta posterior (ScP-), which are separated at the base but adjacent or fused for most of their lengths, thus strengthening the anterior margin; radius anterior (RA+), which is closely associated with ScP and C and divided into 2 branches beyond the middle of the wing (the base of RA is reduced in Polyphaga); radius posterior (RP-), which is deeply concave and tends to become desclerotised proximally, so that its basal connection is often lost; media posterior (MP-), a long and strong vein which is primitively forked twice; cubitus anterior (CuA+), which is also forked; and the anal veins, AA+ and AP-, which are separated by the *anal fold*. The precosta (PC) is rarely visible as a soft, flat strip anterior to the costa near the base. The subcosta anterior (ScA+) is strongly sclerotised, superimposed on ScP- and fused with the costa near the base. The media anterior (MA+) in beetles, as in all endopterygotes, is fused with the radius and has become part of RA+. The separation of RA and RP near the base, coupled in a special way with the entry of MA into the base of RA, is an apomorphy of beetles. The base of RP is often reduced, and its connection with RA may be partly concealed by the base of MA, which is transformed into a brace called the *medial bridge*. The cubitus posterior (CuP-) is either absent or very short and fused to the base of AA+. The *claval fold*, which follows the course of CuP, is very short or absent. The anal basivenale is almost completely obscured by a fold. The jugal veins are reduced to one or frequently missing.

The major differences between the system of nomenclature adopted here and that advocated by Forbes, Crowson and others concern the identity of RA and RP, MP and the veins immediately following MP. RA<sub>3+4</sub> in Archostemata and Adephaga is called the 'radial sector' (p. 16) or 'sector' (Hamilton 1972b; Ward 1979); however this term in Polyphaga has been applied to a cross-vein (see below). The major vein, MP<sub>1+2</sub> has been called the cubitus by most workers, but there has been little agreement on the names of those veins immediately following it. What is here referred to as MP<sub>3+4</sub> has been called



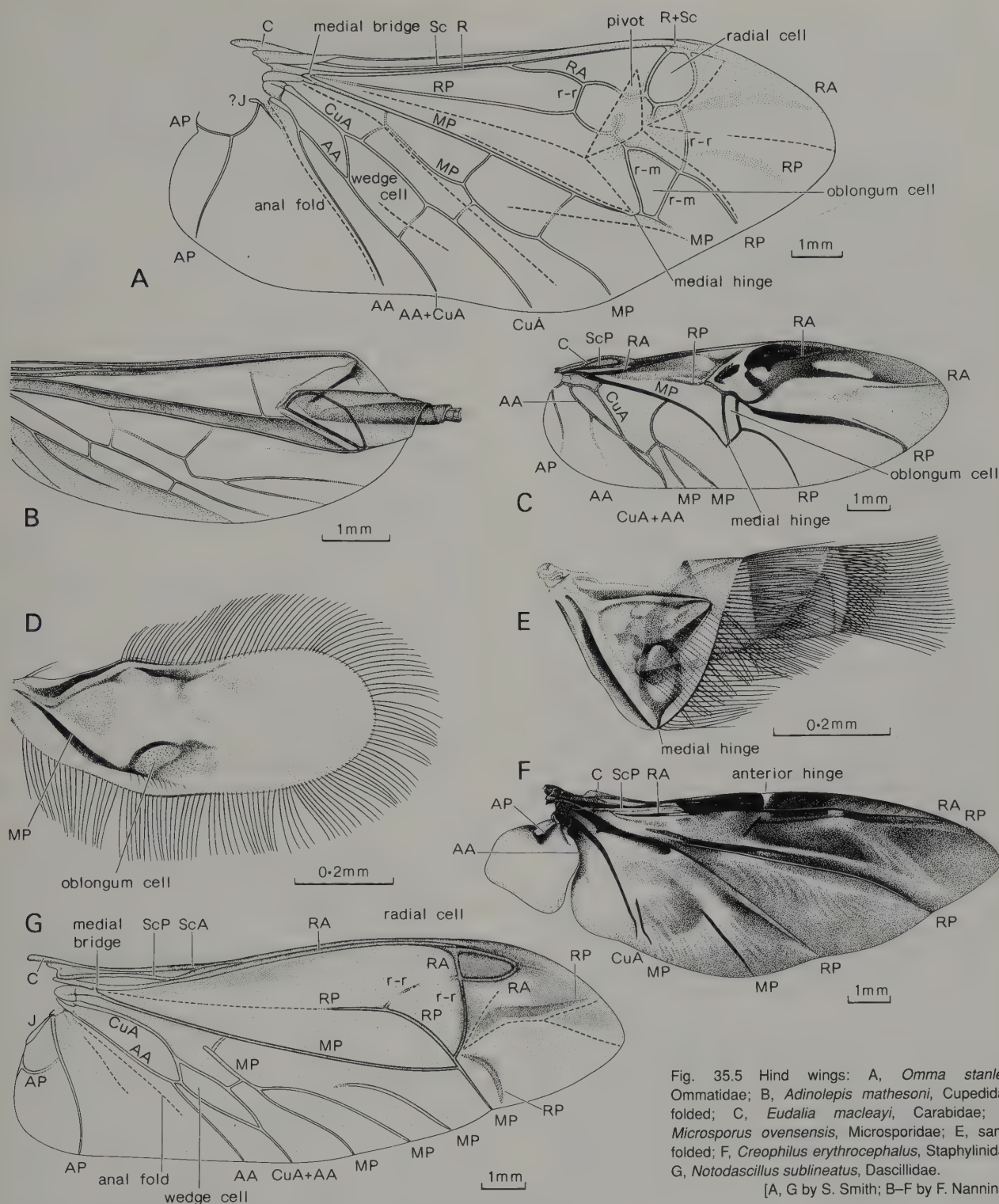


Fig. 35.5 Hind wings: A, *Omma stanleyi*, Ommatidae; B, *Adinolepis mathesoni*, Cupedidae, folded; C, *Eudalia macleayi*, Carabidae; D, *Microsporus ovensensis*, Microsporidae; E, same, folded; F, *Creophilus erythrocephalus*, Staphylinidae; G, *Notodascillus sublineatus*, Dascillidae.

[A, G by S. Smith; B-F by F. Nanninga]

Cu<sub>2</sub> by Ponomarenko (1972) and 'plical' by Hamilton (1972b). CuA, which immediately follows, was called 'empusal' by Hamilton. Forbes (1922) and Crowson (1955, 1981) refer to all veins behind our MP as anal veins.

A number of cross-veins and cells occur in most Archostemata and Adephaga, but only a few are retained in Polyphaga. In most beetles cross-veins between the

branches of RA form the *radial cell*, which often houses the *pterostigma* (p. 12). In Archostemata (Fig. 35.5A) there may be 4 cross-veins between RA and RP, but some tend to be obscured by the folding pattern. In Polyphaga only two of these are attached to the radial cell; one usually connects the cell to RP, while the other loses its connection to RP and becomes elongated and longitudinally oriented in some Elateriformia. For this reason the cross-

vein has been called the 'radial sector' or 'radial recurrent'. RP is often connected to MP by cross-veins, two of which enclose the *oblongum cell* in most Archostemata, Adephaga and Myxophaga. In Polyphaga, one of these cross-veins forms with the distal remnant of RP the *radio-medial loop* ('medial recurrent' of Forbes 1922 and 'medio-cubital loop' of Crowson 1955). Several cross-veins may occur behind MP, but the only cell which has been consistently named is the *wedge cell* (or 'anal cell'), formed within the fork of CuA. Another feature occurring in various unrelated groups (e.g. Amphizoidae, Noteridae, Dytiscidae, Trachypachidae and many groups of Cucujoidea and Tenebrionoidea) is the pigmented patch located just behind and near the apex of MP and usually formed of scale-like microtrichia. This structure is called the 'subcubital fleck' by Crowson (1955, 1981) and 'subcubital binding patch' by Hammond (1979), who contends that it may serve to hold that portion of the wing in place during folding by interlocking with a similar patch beneath the elytra. Considering its proximity to MP as defined here, the term *medial fleck* is a more appropriate name for the structure. Reduction in venation occurs throughout the order, especially in very small beetles, and usually involves the loss of cross-veins and the reduction or loss of RP and some of the veins behind MP. It is interesting that the medial fleck remains intact in some brachypterous wings, in which almost all venation has disappeared.

Because folding has a profound effect on the nature of wing venation in Coleoptera, the two major wing types in beetles are based primarily on the folding mechanism. The *adephagan* type, which occurs in Archostemata, Myxophaga and Adephaga, is characterised by having the major transverse fold crossing  $MP_{1+2}$  at a point called the *medial hinge* (Figs 35.5A–E) just proximal to the first radio-medial cross-vein; during folding the oblongum cell, if present, is displaced. This type of wing is also characterised by having the major pivotal area (areas C and D or C + D of Forbes) occurring proximal to the radial cell and, in general, having more complete venation. In the *polyphagan* type of wing, the transverse fold does not cross MP (so that the medial hinge is absent), the oblongum cell is never present, the major pivotal area lies distal to or just below the radial cell and the venation is often more reduced. Within the Polyphaga further reduction occurs in several lineages, especially Staphylinoidea (Fig. 35.5F), Scarabaeoidea and Cucujiformia (Fig. 35.5G). Wing folding patterns were studied in detail by Forbes (1926) in an attempt to utilise them at the supra-generic level; although many of his tentative groupings were later substantiated using other data, some were found to represent grades rather than clades (Hammond 1979).

Wings in Coleoptera are frequently atrophied to a greater or lesser extent, and this is a common phenomenon in island or mountain-top species (Darlington 1943). The wings may be shortened and not folded (brachypterous), reduced to mere vestiges (micropterous), or completely absent (apterous). Wing polymorphism, which has been reviewed by Hammond (1985), is com-

mon in various families, and is most frequently under genetic control. Some beetles with fully developed wings may be unable to fly because of the degeneration of flight muscles during the life of the insect associated with the development of the gonads (Jackson 1956; Langor 1987). In very small beetles, such as Microsporidae (Figs 35.5D, E) and Ptiliidae (Fig. 35.24A) the wings are commonly fringed with long setae; the wing surface in these species is highly reduced and the setae have taken over its function.

**Abdomen.** The abdomen is usually composed of 10 segments in the male and 9 in the female, but 9 is modified forming the *genital segment* and 10 in the male is often highly reduced or fused to 9. If one excludes the genital segment, 8 terga can be counted on the dorsal surface of the abdomen in most adult beetles. Although the terga are less easily traceable in some flightless species, their number is readily determined by counting the spiracles starting with the enlarged one at the base of the abdomen (Figs 35.6C, 12). Each tergum has a major plate called a *tergite*, which may or may not be flanked by an additional pair of sclerites called *laterotergites*. The spiracles are usually located in the pleural membrane, and there may be an additional sclerite (*parasternite*) between the spiracle and the inflexed portion of the sternum (*laterosternite*) (Fig. 35.6C). The first 5 or 6 tergites in most beetles are lightly sclerotised, but the last few may be hardened when they are exposed beyond the elytral apices; in these cases, the apparent terminal segment (7 or 8) is called the *pygidium* and the one preceding it the *propygidium*. More tergites are heavily sclerotised in beetles with very short elytra (e.g. Staphylinidae) but also in some having complete elytra (e.g. some Buprestidae).

In almost all beetles sternites 3 to 7 are sclerotised and visible externally in the intact specimen (Figs 35.6A–C); sternite 1 is absent or rarely represented by a small sclerite concealed by the hind coxae, 2 is often visible only laterally (often hidden beneath the edges of the elytra), and 8 is often retracted along with the genital segment (9). Those sternites which are externally visible are called *ventrites*, and their number is often used as a key character. Most commonly 5 (S3 to S7) are visible; 6 occur when S2 is visible or S8 exposed at the abdominal apex, 7 when both conditions occur together, and 8 only in males of some groups (e.g. *Pheropsophus* in Carabidae, Hydraenidae, Lycidae, Cantharidae) in which S9 is also exposed.

Ventrites may be joined by membrane (exposed or concealed by the overlapping of the sternites) and capable of free movement, but in many families the basal 2 or 3 ventrites are *connate* (immovably joined together) and in a few groups, such as Eucnemidae, Throscidae or Anthribidae, 4 or even 5 may be connate. The degree of connation varies considerably and there is a graded series from free and overlapping ventrites to those which are abutting and solidly fused, with a weak or incomplete suture between them. In most members of the family Aderidae, the suture between the first two ventrites is virtually absent, so that there appear to be only 4 ventrites. The lateral edges of the ventrites in many groups are



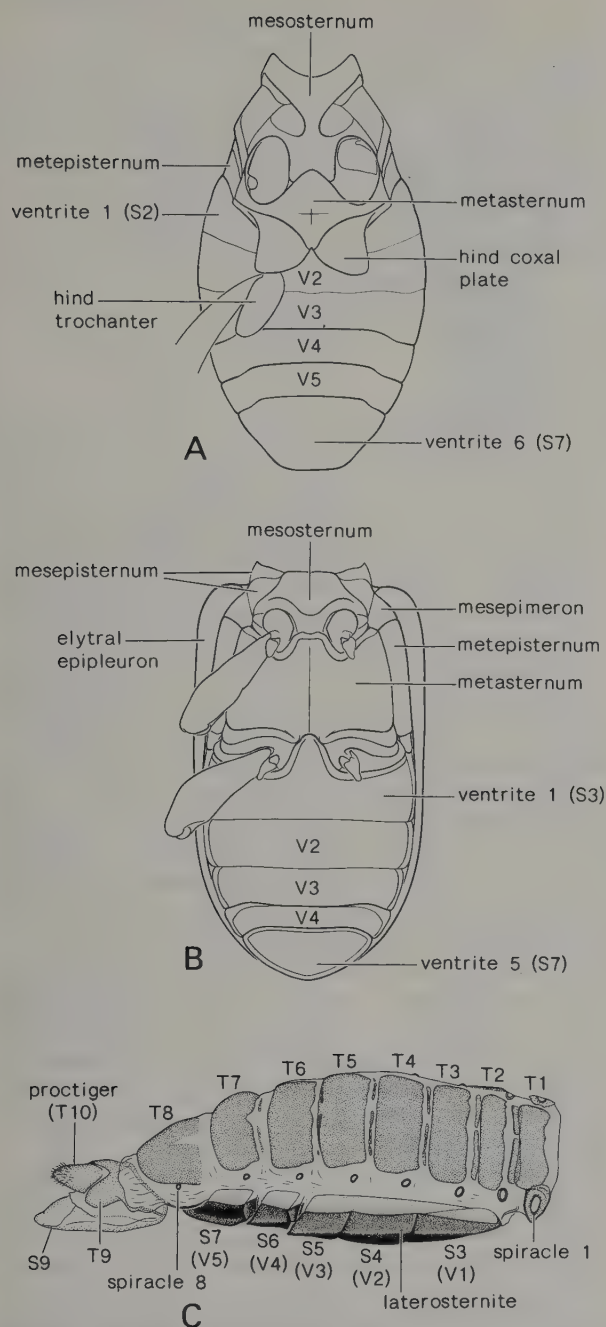


Fig. 35.6 Pterothorax and abdomen, ventral: A, *Pamborus guerinii*, Carabidae; B, *Meneristes intermedius*, Tenebrionidae. C, *Rhinorhipus tamborinensis*, Rhinorhipidae, male abdomen (with aedeagus removed), dorso-lateral. [A, B by S. Smith; C by S. P. Kim]

modified to form interlocking devices with the elytra; these and also the nature of ventrite junctions have been discussed in detail by Kasap and Crowson (1975). Ventrite 1 often bears straight or curved *femoral lines* (Figs 35.48j, 49d), like those on the metasternum, and in males of some species *sex patches* (groups of secretory setae) occur on the basal one or more ventrites or occasionally elsewhere (Faustini and Halstead 1982; B. A. Holloway 1985). The last ventrite is also modified in many species. The free edge may be crenulate to serve

as an interlocking device with the elytral apex (as in Cerylonidae, Fig. 35.15BB) or variously modified in males to accommodate the extrusion of the aedeagus during copulation. In females of cryptocephaline Chrysomelidae a cavity on the last ventrite assists in the formation of the faecal egg case.

The basic number of functional spiracles on the abdomen is 8, but in a number of groups those on segment 8 become reduced or absent, and those on the preceding one or two segments may also be atrophied; in Hydrophilidae and some Staphylinidae, however, apical spiracles may be functional while one or more intermediate ones have become atrophied. There are never more than 7 pairs of functional spiracles in Cucujiformia and Hydrophiloidea, many Staphylinidae and Scarabaeoidea, most Psephenidae, Scirtidae and a few other groups. Although spiracles are usually located in pleural membrane, they may be on the tergites in some Scarabaeoidea and Staphylinidae, or on the sternites in some members of the former group.

**TERMINALIA.** The *genital segment* or ano-genital complex in beetles appears to be most complete in males of some Scarabaeoidea and Elateriformia (Figs 35.6c, 7, 8A), where T10 exists as the *proctiger* just above the anus and segment 9 forms a ring-like structure to which the genitalia are attached. The genital segment is sometimes called the *genital capsule* when it forms a tube surrounding the aedeagus, but that term has also been applied to a capsule formed by T8 in some Cucujoidea (e.g. Nitidulidae). In most males and females, T9 is either divided at the midline (Fig. 35.8A) or separated into two apparently disconnected pieces called *paraprocts* (Fig. 35.9A). Further modifications include the fusion of T9 and T10 forming a simple ring, and the anterior extension of S9 forming a ventral strut, the *spiculum gastrale* (Fig. 1.31c), which usually has a fork at the posterior end; in some groups (e.g. Chrysomeloidea, Curculionoidea) the tergal portion of the genital segment becomes desclerotised so that only the ventral strut remains. Crowson (1981) disagrees with the interpretation given above; he considers the proctiger to represent T9 and the lateral sclerites to be laterotergites of segment 9 which have fused in front of the proctiger in those forms here considered to represent the basal condition (see also Hieke 1966, 1971). Based mainly on a study of Adephaga, Deuve (1988) concluded the genital 'ring' is composed only of laterotergites and that sternites 8 and 9 are absent in adults of both sexes throughout the Coleoptera.

**MALE GENITALIA.** The male copulatory organ, here called the *aedeagus*, is a development of the posterior end of the ejaculatory duct, which opens behind S9 (Fig. 35.7) and consists of three parts: the basal *tegmen*, which may be composed of a *phallobase* (*basal piece*) and paired *parameres* (*lateral lobes*); the *penis* (*median lobe*), which is usually more or less enclosed at the base by the tegmen; and the *internal sac* (*endophallus*), which is primarily membranous but may be armed with a variety of spicules and sometimes a long, sclerotised *flagellum*, at the end of which is the *primary gonopore*. The penis is attached to the tegmen by means of the *first connecting*

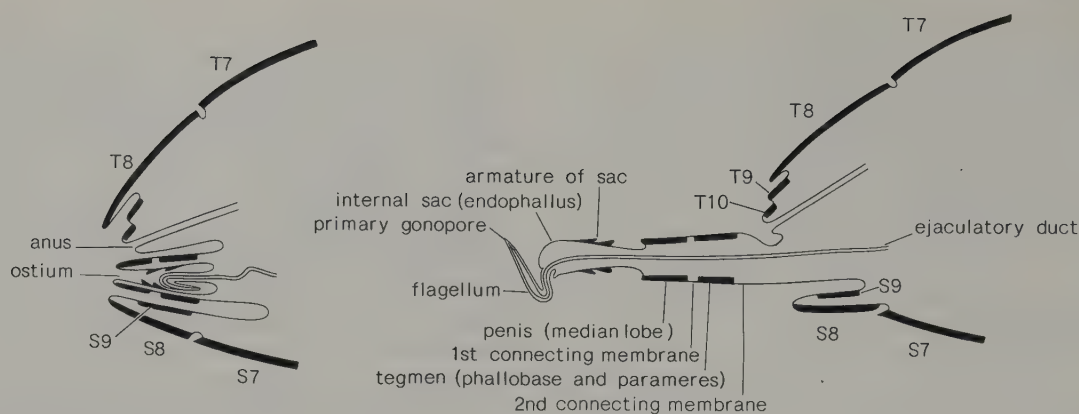


Fig. 35.7 Abdominal apex of male, diagrammatic sagittal sections: A, with aedeagus retracted; B, with aedeagus evaginated.

[F. Nanninga]

membrane, and the tegmen is attached to the 9th segment by means of the *second connecting membrane*. During copulation, the internal sac is extruded through an opening, the *ostium*, at or near the end of the penis, and enters the female vagina with the flagellum extending anteriorly to reach the spermatheca (see below). Although the term aedeagus is used here in the broad sense, following Crowson (1981), Snodgrass (1963) restricted the term to what is here called the penis and used the term *phallus* for the entire copulatory organ. Some authors (Michener 1944; Wood 1952) have homologised the phallobase with the fused *gonocoxites* and the parameres with the *gonostyli* of the female ovipositor.

The *trilobed* aedeagus, generally considered to be the most primitive type in beetles, consists of a ventrally sclerotised phallobase to which a pair of freely articulated parameres are attached, and a simple penis lying above it (Figs 35.8A, B). From this basic type, it is possible to derive the variety of aedeagal types present within the various coleopteran lineages. A common modification has been the reduction or loss of the phallobase, so that the parameres appear to articulate directly with the penis; this condition occurs in Archostemata, most Myxophaga and Adephaga, and many Staphylinoida. Another common modification is the fusion of the two parameres to form a single tubular piece enveloping the penis, as in most Histeridae and Buprestidae. In most members of the Bostrichoidea, the phallobase is retained, but the parameres are more or less fused to the base of the penis (Fig. 35.8c). The greatest diversity of genitalic types occurs within the Cucujiformia, and Crowson (1955) proposed a series of possible evolutionary changes by means of which such an array of structures could have been derived. The parameres may be fused with the phallobase and the tegmen may form a tubular structure enveloping the penis; this is the *sheath type* of aedeagus, in which there are usually a pair of anterior tegminal struts resulting in the *double tegmen* (Fig. 35.8D) of Crowson (1964b). This condition is characteristic of Cleroidea but also occurs in the cucujoid families Biphylidae and Byturidae.

A more common type, occurring throughout the Cucujoidea, is the *ring type* or *cucujoid* aedeagus, in which the phallobase forms a ring around the penis, often

with the parameres articulating posteriorly with the dorsal portion (Fig. 35.8F) and a median tegminal strut extending anteriorly from the ventral portion (Fig. 35.8G). The ring section is often referred to as the tegmen in cucujiform beetles, and the parameres are considered by some to be secondary developments, which are not homologous to the parameres of the trilobed aedeagus. In Coccinellidae (Fig. 35.8G), there is also a median tube-like process extending posteriorly between the parameres and serving as a guide for the penis; coccinellid workers refer to the guide as a *basal lobe*, the entire tegmen as the *phallobase*, the median tegminal strut as the *trabes*, and the penis as the *sipho* (Gordon 1985). Further modifications of the cucujoid aedeagus include the reduction of the ring segment, fusion or disappearance of the parameres and narrowing of the strut (Fig. 35.8I), as in many Chrysomeloidea and Curculionoidea, and finally in these same groups the desclerotisation of the dorsal region, so that only a posteriorly-forked strut remains beneath the penis. The penis in this type of aedeagus may be divided into a ventral *pedon* making up the body and the *tectum*, which forms a dorsal lid over the ostium (B. A. Holloway 1982).

Another modification of the sheath type of aedeagus involves the desclerotisation of the ventral portion of the tegmen, so that its sclerotised body lies entirely above the penis; this results in something like an inverted trilobed type, although in most cases the parameres are fused into a single piece; this *heteromeroid type* occurs throughout the Tenebrionoidea. Further inversion by rotation about the longitudinal axis may also occur, so that the tegmen lies below the penis, in various tenebrionoid groups, including Mordellidae, Rhipiphoridae, Ciidae, Monomidae, Colydiidae, Zopheridae, some Tenebrionidae, Prostomidae, Oedemeridae, Mycteridae and Aderidae. In Pythidae and Salpingidae, there are almost always a pair of *accessory lobes* (Fig. 35.8H) attached to the tegmen but not considered to be homologous to parameres. [Crowson 1984; Iablokoff-Khnzorian 1980]

**FEMALE GENITALIA.** The female ovipositor consists of a pair of appendages attached ventrally to the paraprocts, and each appendage is composed of a basal *gonocoxite* or *coxite*, which is often divided into 2 or more parts, and an apical *gonostylus* or *stylus*. Various other terms, such as



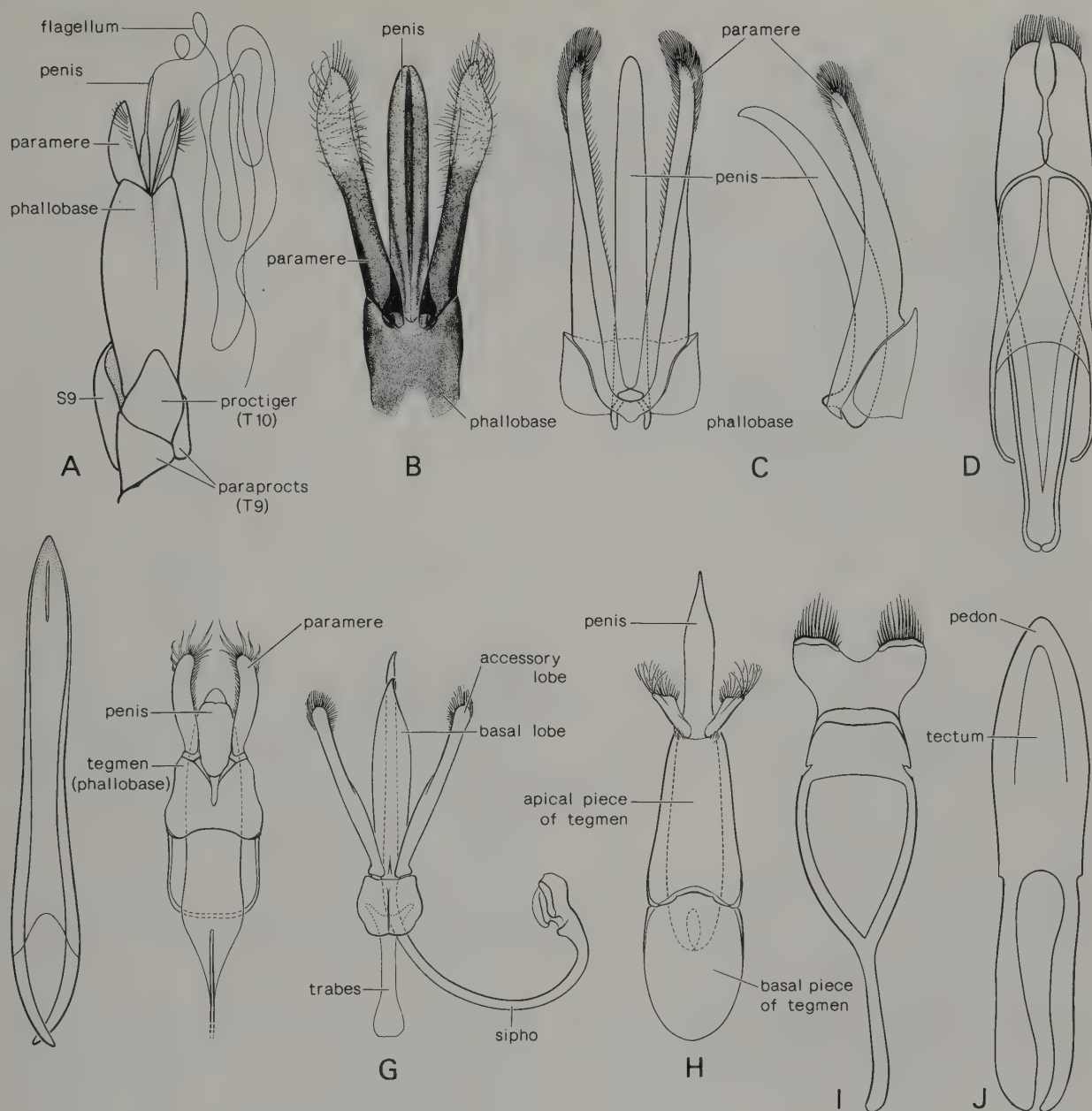


Fig. 35.8 A, *Lamprima aurata*, Lucanidae, male abdominal apex with aedeagus everted, dorsolateral. Aedeagi: B, *Rhinorhipus tamborinensis*, Rhinorhipidae, ventral; C, *Dermestes maculatus*, Dermestidae, dorsal, lateral; D, E, *Lepidopteryx decorata*, Trogossitidae: D, tegmen, dorsal; E, penis, dorsal; F, *Passandra* sp., Cucujidae, dorsal; G, *Epilachna guttatopustulata*, Coccinellidae, dorsal; H, *Morpholycus costipennis*, Pythidae, dorsal; I, J, *Eurhynchus laevior*, Brentidae: I, tegmen, dorsal; J, penis, dorsal.  
[A by F. Nanninga; B by S. P. Kim; C–J by S. Smith]

*valvifer* and *hemisternite* have been proposed for the basal element of the gonocoxite, but these have not been used consistently by different authors. In very long ovipositors, which occur in beetles which lay their eggs deep in a substrate like rotten wood, the entire 9th segment is drawn out, so that the proctiger forms a long pair of sclerotised rods and the paraprocts are similarly extended and provided with sclerotised rods called *baculi* (Fig. 35.9c). Short ovipositors with heavily sclerotised coxites and reduced styli (Figs 35.9b, d) are often used to dig in soil, while longer, sclerotised ovipositors may serve to cut egg cavities into plant tissue. Highly reduced

ovipositors are usually found in those species which lay their eggs on an exposed surface. The classical comparative work on the beetle ovipositor is that of Tanner (1927), while several recent works (Bils 1976; Burmeister 1976, 1980) have concentrated on the suborder Adephaga. In addition, Mickoleit (1973) compared the structure of the beetle ovipositor with that of various neuropteroid orders. [Lindroth 1957, Iablokoff-Khnzorian 1974]

**Internal Anatomy.** The space enclosed dorsally by the clypeus and labrum-epipharynx, ventrally by the labium-hypopharynx, and laterally by the maxillae and mandibles

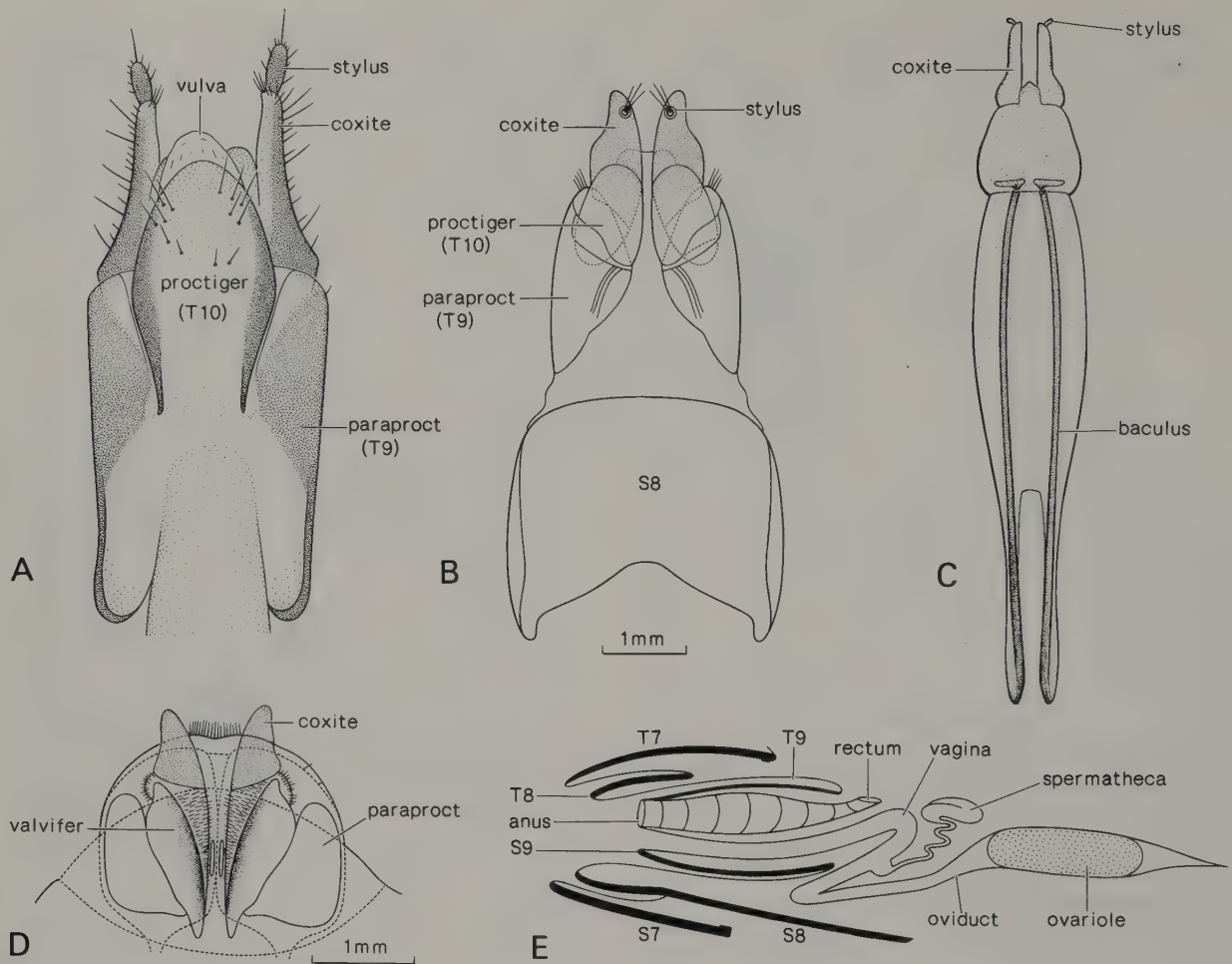


Fig. 35.9 Ovipositors: A, *Rhinorhipus tamborinensis*, Rhinorhipidae, dorsal; B, *Ptomaphila lacrymosa*, Silphidae, ventral; C, *Byrrhocryptus variegatus*, Ptilodactylidae, ventral; D, *Calosoma schayeri*, Carabidae, ventral. E, Abdominal apex of female *Atomaria* sp., Cryptophagidae (diagrammatic section).

[A by S. P. Kim; B, D by F. Nanninga; C by S. Smith; E after M. E. G. Evans 1961c]

is called the *preoral cavity*, since it lies outside the true opening of the alimentary canal. The proximal portion of this cavity, the *cibarium*, and the anterior end of the fore gut, the *pharynx*, are capable of being distended by a series of dilator muscles attached to the walls of the clypeus and frons, respectively, and one or both may form a pump in liquid-feeding species. Salivary glands of various types have been reported opening near the bases of the mandibles and maxillae (Srivastava 1959), and paired silk-producing glands occur at the base of the labium in larvae of the South African tenebrionid *Parastizopus armaticeps* (Schulze 1975). The pharynx is joined to the *oesophagus*, which may extend to the mid gut without modification or form a distended storage organ, the *crop*. The end of the fore gut is usually blocked by a valve, the *proventriculus*, which controls movement of food into the mid gut but may also contribute to food processing. Forsythe (1982) has shown that there is a correlation between proventricular structure and the nature of the food mass (e.g. animal or plant, solid or liquid) in Carabidae.

The mid gut varies considerably in length and complexity. In many beetles the entire mid gut may be cov-

ered with small papillae known as *regenerative crypts* or with larger diverticula called *gastric caeca* (Fig. 35.11). A second valve, the *pyloric valve*, indicates the beginning of the hind gut, which consists of an *ileum*, *rectum* and *anus*. The Malpighian tubules, which open into the hind gut near the pyloric valve, are usually 4 or 6 in number. The ends of the tubules may be free, but in all Cucujiformia and most Bostrichoidea they are attached to the wall of the rectum, an arrangement known as *cryptonephric* or *cryptonephridial* (Saini 1964). *Pygidial glands*, which are usually paired, occur in most Adephaga, some Staphylinidae, many Tenebrionidae and members of various other groups; these glands are usually defensive in nature, producing a variety of organic acids, aldehydes, ketones, quinones and other substances. Their reservoirs usually open just behind the 7th or 8th segments. In the carabid subfamilies Paussinae and Brachininae, a pair of complex, 2-chambered glands eject a pungent, corrosive fluid, which is expelled explosively (pp. 92, 614). In Gyrinidae (p. 616) and stenine Staphylinidae (p. 623), the pygidial glands secrete surfactants, which are used to propel the beetle on the surface of water.

The basic number of ganglia comprising the central



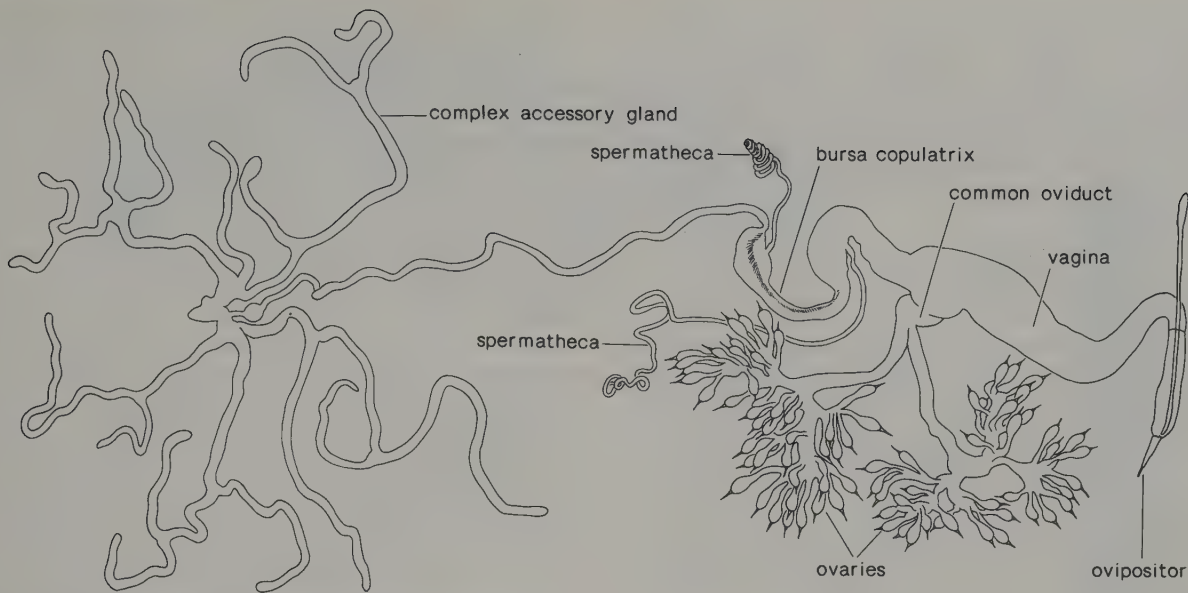


Fig. 35.10 *Agrypnus caliginosus*, Elateridae, female reproductive system.

[A. Calder]

nervous system is 3 thoracic and 8 abdominal with double connectives between them, but in most beetles the number is reduced due to the fusion of the apical abdominal ganglia and the first abdominal with the metathoracic; the number of abdominal ganglia may be as few as 1 in Histeridae, Scarabaeidae and Curculionidae.

In the male reproductive system, each vas deferens may be enlarged to form a *seminal vesicle* and may be associated with a *spermatophoral gland* and *accessory gland*. The presence of these glands and their form varies considerably within the order. The testes consist of a single coiled tube in Adephaga, but in Polyphaga and Archostemata there are a number of separate follicles, which may be sessile or pedicellate (joined to the vas deferens by individual vasa efferentia).

The female reproductive tract begins at the *vulva* (Fig. 35.9A) and continues as the *vagina*, which may be enlarged and modified to form a *bursa copulatrix*; the common oviduct, one or more *spermathecae* and usually an *accessory gland* or *spermathecal gland* open into the bursa or vagina (Fig. 35.9E). In Elateridae and some other groups (Fig. 35.10), the bursa is often armed with a series of spines or sclerites and the accessory gland is very large and complex. An additional pair of glands, the *colleterial glands*, may be located near the opening of the genital tract, and are associated with chorion formation. The ovarioles in Adephaga are *polytrophic*, with each oocyte being provided with its own nutritive cells; those in all Polyphaga studied (Büning 1979) and in the archostematan genus *Micromalthus* (Scott 1941) are *telotrophic*, with a single mass of nutritive cells located at the apex of the ovariole.

Comparative studies of internal anatomy have added significantly to the number of characters available for phylogenetic analysis. Some recent works include: Calder (1989, 1990) (Australian Curculionoidea); Ekis and Gupta (1971) (alimentary canal of Cleridae; see Crowson

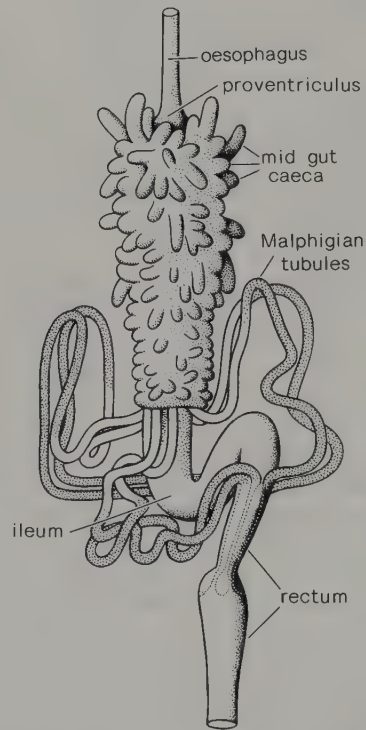


Fig. 35.11 Alimentary canal of *Atomaria* sp., Cryptophagidae.

[After M. E. G. Evans 1961a]

1972a); Kasap and Crowson (1975) (Elateriformia); Kasap and Crowson (1977) (Curculionoidea); and Mann and Crowson (1983) (Chrysomeloidea).

**Karyotype.** The most common and probably ancestral chromosome complement in Coleoptera is 9Xyp, i.e. 9 pairs of autosomes and a very small y chromosome, which unites with the much larger X at meiosis to form a parachute-like figure. The diploid number varies from 4

to 69, and sex determination is also variable, with the y chromosome being lost in several groups, including Elateridae, Cantharidae, Lampyridae and Lycidae. Male haploidy occurs in the archostematan *Micromalthus debilis* and in some members of the genus *Xyleborus* (Curculionidae: Scolytinae). [Crowson 1981; Petitpierre and Segarra 1985; Smith and Virkki 1978]

### Immature Stages

**Egg.** In most cases, the eggs are simple, ovoid and without surface ornamentation, but a sculptured chorion is known in Cupedidae and in some groups, like paropsine Chrysomelidae (De Little 1979), which lay their eggs on surfaces. Eggs of cryptocephaline Chrysomelidae are enclosed by a layer of faeces called a *scatoshell*. Hatching is often initiated by *egg-bursters* or *hatching spines*, which may be present on the head (e.g. in Hydraenidae, Hydrophilidae, some Staphylinidae) or on thoracic or abdominal terga (e.g. in some Staphylinidae, Histeridae, Scarabaeoidea and many Cucujiformia) of the 1st instar larva (van Emden 1946). [Hinton 1981]

**Larva.** Larvae of Coleoptera are usually distinguished from those of most other endopterygotes by the following features: 1) well-developed and usually sclerotised head capsule; 2) no adfrontal ridges (paired endocarinae forming a V between the ecdysial lines) (p. 829); 3) antennae with 4 or fewer segments; 4) 6 or fewer stemmata; 5) mandibles of the chewing type, opposable in a transverse plane; 6) median labial silk gland or spinneret absent; 7) abdomen without ventral prolegs bearing crochets; 8) respiratory system usually peripneustic and never with a functional metathoracic spiracle; and 9) spiracles, if cribriform, never with the ecdysial scar completely enclosed by the sieve plate. The 1st instars of Strepsiptera resemble triungulins of Meloidae and Rhipiphoridae, but they differ in lacking mandibles, antennae, labial palps and trochanters.

Larvae of Trichoptera, Megaloptera, Raphidioptera and Neuroptera differ from most beetle larvae in having 6-segmented legs, and those beetles which do have an additional leg segment differ from members of the first three orders in having a sclerotised ligula (Archostemata) or fused labrum (Adephaga), and from the last in the possession of mandibulate mouth-parts and labial palps. Larvae with 6-segmented legs also occur in Nannochoristidae (MECO), but they have more than 6 pairs of stemmata and panorpoid spiracles (with the sieve plate surrounding

the ecdysial scar). Lepidopterous larvae are most often confused with those of beetles, but they almost always have a median labial gland developed into a spinneret, paired adfrontal ridges, and crochet-bearing prolegs on S3 to S5 or S6 and S10 (p. 829). It is very rare to find a lepidopterous without at least one of these three features, but in the primitive moth family Micropterigidae, in which adfrontal ridges and spinneret are both lacking, the prolegs are atypical, being simple and similar to those in Mecoptera; these larvae may be recognised by their unusual form (hexagonal in cross-section), retracted head, 3-segmented legs and characteristic, thickened setae.

Larvae of Siphonaptera, nematoceran Diptera and higher Hymenoptera are often confused with legless larvae of Curculionidae and certain other families. Those of the first two groups differ from most apodous beetle larvae in being elongate and narrow, with a prognathous head and a different type of spiracular system (holopneustic, amphipneustic or metapneustic and with a panorpoid type of spiracle or a cribriform type with 3 openings). Apodous Hymenoptera, on the other hand, often differ in having a labial gland, 2 pairs of thoracic spiracles, and reduced maxillary and labial palps; the characteristic trident sclerite on the labium of weevil larvae also distinguishes them from larvae of Hymenoptera or other orders.

Larvae of Symphyta (HYMN) usually have well-developed legs and resemble many beetle larvae; most of them are distinguished by the presence of paired prolegs on segments 2 to 7 or 8 (and usually 10). Some Pergidae lack prolegs but have a single pair of large stemmata, dome-like, unsegmented antennae and an obvious metathoracic spiracle. Xiphydriid and siricid larvae have vestigial legs and a spine-like process on the abdominal apex, as in the beetle family Mordellidae; they differ from mordellids in having elongate-elliptical spiracles. Further distinctions between beetle larvae and those of other orders may be extracted from the key in Chapter 1.

The beetle larva has a well-developed head, 3 thoracic segments and usually 10 abdominal segments (sometimes reduced to 9 or 8). The thoracic segments are rather similar, although the first is sometimes enlarged and more heavily sclerotised. Abdominal segment 10 is relatively small, surrounds the anus, and sometimes bears one or more ventral *pygopods*. Segment 9 is often armed with paired processes, called *urogomphi*, which have evolved a number of times in Coleoptera and are not homologous to the cerci of some other insect orders.

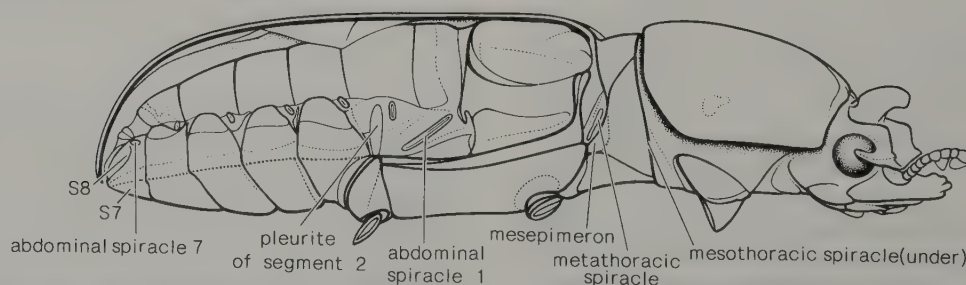


Fig. 35.12 *Aulacocyclus collaris*, Passalidae, right elytron and hind wing removed to show disposition of spiracles.

[F. Nanninga]



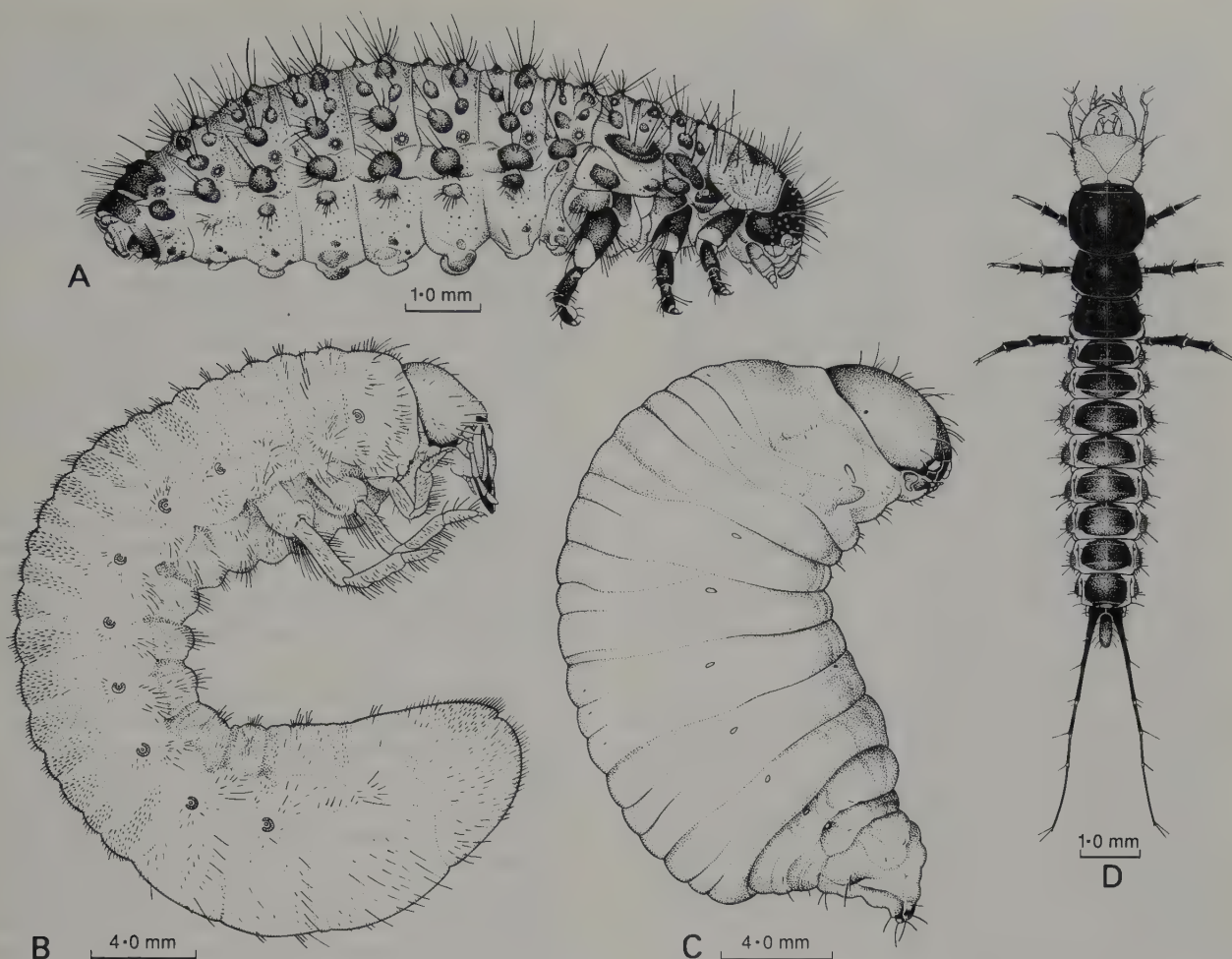


Fig. 35.13 Larval types: A, *Paropsisterna beata*, Chrysomelidae (eruciform); B, *Anoplognathus pindarus*, Scarabaeidae (scarabaeiform); C, *Trigonotarsus rugosus*, Curculionidae (apodous); D, *Eudallia macleayi*, Carabidae (campodeiform). [F. Nanninga]

A number of purely descriptive terms are commonly used for general body types associated with particular modes of life. *Campodeiform* larvae (Fig. 35.13D) are active and usually predatory, with a prognathous head, long thoracic legs and well-developed, more or less posteriorly oriented, 1- to many-segmented urogomphi; most Carabidae and Staphylinidae have this type. *Eruciform* larvae (Fig. 35.13B) are less active, cylindrical or slightly flattened forms with short legs and without or with short urogomphi; Tenebrionidae and Chrysomelidae have many examples of this type. The *scarabaeiform* type (Fig. 35.13B) is a C-shaped, rather long-legged grub characteristic of Scarabaeoidea and often found in soil or rotten wood. The *apodous* type (Fig. 35.13C) lacks thoracic legs and urogomphi and has reduced antennae and palps; examples are found throughout the Curculionoidea. These general categories do not readily accommodate a number of peculiar larval types, such as the flattened and disc-like larvae of Psephenidae (Fig. 35.39G), some Corylophidae (Fig. 35.49H, I) or murmidiniine Cerylonidae (Fig. 35.50J); the *onisciform* type, which is ovate and flattened with lateral processes, as in Brachypsectridae (Fig. 35.39H) or *Priastichus* (Fig. 35.50B); or the elongate, strongly flat-

tened, subcortical larvae found in the families Cucujidae (Fig. 35.50D) or Pythidae (Fig. 35.52I).

The most common type of larval head is *prognathous*, with the mouth-parts directed anteriorly, and *protracted*, with the head not or only slightly retracted within the thorax (Figs 35.13D, 50A-F); in a few groups, such as Buprestidae, Bostrichidae, Cerambycidae and Belidae, the head is prognathous and strongly *retracted* into the thorax (Figs 35.16A, 39A, 60A), and in a number of others, including Scarabaeoidea, Anobiidae, Chrysomelidae and Curculionidae, the head is strongly declined or *hypognathous*, with the mouth-parts directed ventrally (Figs 35.13A-C, 50G, 60C, D). The *ecdysial line*, often called the *epicranial suture*, is usually more or less Y-shaped, with a median *epicranial stem* (or *coronal suture*) and a pair of *frontal arms* (or *frontal sutures*), which may be doubly curved (Figs 35.16I, K), in which case they are called *lyriform*. The frontoclypeal suture is often absent, so that there is an undifferentiated *frontoclypeal region*, and the labrum in some groups is partly or completely fused to the head capsule, forming a *nasale* (Fig. 35.16I). A single *endocarina* often extends beneath the epicranial stem, if present, and usually between the frontal arms

(Figs 35.16H, J–L); but in some larvae *paired endocarinae* may extend beneath the frontal arms (Fig. 35.16M).

The antennae are usually 3-segmented with a *sensorium* located at or near the apex of the penultimate segment (Figs 35.16O, P). Adephaga and Archostemata often have 4-segmented (or rarely 5-segmented) antennae, Scirtidae have more than 5 antennal segments (multiannulate flagellum), and reduction to 1 or 2 segments has occurred in a number of groups, including Passalidae, Rhipiceridae, Buprestidae, Callirhipidae, Lycidae, Anobiidae, Coccinellidae, Mordellidae, Chrysomeloidea and Curculionoidea. Stemmata vary from 1 to 6 on a side and may be highly reduced or absent in many larvae inhabiting substrates such as wood or soil.

Larval mandibles are quite variable and have been used extensively in keys and descriptions. The apex may be simple and rounded, acute, or composed of 2 to several teeth or lobes, and the incisor area may have a sclerotised tooth, the *retinaculum* (Fig. 35.16R). The base of the mesal edge is often enlarged forming a *mola*, which may be armed with asperities (Figs 35.17C–E) or transverse ridges (Figs 35.17A, B, H), and a projection known as the *accessory ventral process* may occur on the ventral surface just proximad of the mola (Figs 35.17B–E). Sometimes a mola-like structure or *pseudomola* may be located away from the base of the mandible (Fig. 35.16DD). The base of the dorsal surface may bear a patch of microtrichia, usually arranged in rows (Fig. 35.17H); these interact with cibarial plates to move particles towards the mouth (Lawrence 1989, 1991). When a mola is present, there is often a hyaline or membranous (sometimes complex) *prosthema* (Figs 35.17A–E) between it and the apex. In a number of groups, the mola is absent but there may be one or more hyaline processes or tufts of hairs in its place; the terms *lacinia mandibulae* and *lacinia mobilis* are often applied to these structures but the same terms have also been used for the prosthema. In most phytophagous and predatory larvae the mola has been lost, but the mandibles are otherwise very different, those of the former group being heavy and blunt (Figs 35.16BB, CC) or multidentate (Figs 35.16AA, EE) and those of the latter being narrow and falcate (Figs 35.16R, S) and sometimes perforate (Fig. 35.16T). In larvae of Lycidae each mandible is divided longitudinally to form 2 blades (Fig. 35.16Q), and in a few groups (e.g. cerylonine Cerylonidae and the leiodid *Myrmecholeva*) mandibles are stylet-like and enclosed within a sucking tube (Fig. 35.16G).

The *ventral mouth-parts* (*maxillolabial complex*) consist of the paired maxillae and unpaired labium; these are said to be *retracted* when their bases are attached well behind the mandibular articulations (Figs 35.17K, L, N–P) and *protracted* when they are at about the same level as these articulations (Figs 35.17I, J, M). The *hypostomal rods* are cuticular thickenings (dark lines) extending posteriorly from the maxillary bases (Figs 35.17I, L), and the *ventral epicranial ridges* are raised areas or carinae extending posteriorly from the mandibular articulations (Fig. 35.17N) and usually forming between them a recessed area housing the retracted ventral mouth-parts.

The maxilla is composed of the same basic parts as in the adult, namely the cardo, stipes, palp, galea and lacinia; but in many cases the galea and lacinia are fused to form a single *mala*. In most groups, the maxilla is movable and is joined basally to the labium by a *maxillary articulating area* (Figs 35.17K, L); this area is reduced in protracted ventral mouth-parts and in those retracted types in which the maxillae and labium are connate or solidly fused (Figs 35.17N, P, R, S).

Like that of the adult, the labium is composed of a submentum, mentum and prementum, or *postmentum* and prementum when the first two are fused. The *ligula* lies in between the palps; it varies in size and shape and may form a heavily sclerotised plate in Archostemata (Fig. 35.19E) and Callirhipidae (Fig. 35.17S). The hypopharynx is usually armed with a sclerotised lobe known as the *hypopharyngeal sclerome* (Fig. 35.17Z) in larvae with mandibular molae. The *gular region* usually lies between the ventral mouth-parts and the beginning of the prothorax, but in some groups (e.g. Anobiidae, Mordellidae, Chrysomelidae, Curculionoidea) the gular region is absent and the labium is joined directly to the thorax (Fig. 35.17Q).

The basic number of leg segments in Archostemata and Adephaga is 6 (coxa, trochanter, femur, tibia, *tarsus* and *pretarsus* consisting of 1 or 2 claws), whereas in Myxophaga and Polyphaga, the tarsus and pretarsus have fused forming a *tarsungulus*, so that the legs never have more than 5 segments. Some authors consider the last, claw-like, segment in Polyphaga to be the pretarsus and the preceding segment to be a *tibiotarsus* (fused tibia and tarsus) (see Crowson 1964b, Švácha and Danilevsky 1987). Reduction of the legs has occurred in many groups, and legless larvae are characteristic of a few sphaeridiine Hydrophilidae, almost all Buprestidae and Eucnemidae, many Cerambycidae, a few Chrysomelidae and most Curculionoidea. The fore legs are enlarged and modified for digging in some Tenebrionidae, and stridulatory organs may be formed by the mid and hind legs in several groups of Scarabaeoidea.

Although the larval tracheal system is usually peripneustic, the mesothoracic spiracle is often located between the meso- and metathorax and has migrated on to the prothorax in some Anobiidae and Curculionidae. Reduction in the number of spiracles has occurred in a number of larvae with aquatic habits (Hinton 1947b; see p. 41); among Australian beetle larvae, a *hemipneustic* system occurs in final instars of Hygrobiidae and Haliplidae, a *metapneustic* system occurs in Scirtidae, final instars of Psephenidae and early instars of Noteridae, Dytiscidae and donaciine Chrysomelidae, and an *apneustic* system is found in early instars of Haliplidae, Hygrobiidae, Gyrinidae, berosine Hydrophilidae, Elmidae, Psephenidae and some Ptilodactylidae. Unique systems are known in final instar Noteridae and all instars of Microsporidae, in which there are 8 abdominal but no thoracic spiracles, and in final instars of Gyrinidae, which have spiracles on the first 3 abdominal segments. There is considerable variation in spiracular structure. They may be simple and annular as in adults,



have one or more small accessory openings, as in the *annular-uniformous* or *annular-biforous* types (Figs 35.18DD, EE), have 2 narrow openings separated by a septum, as in the *biforous* type (Fig. 35.18FF), or have the opening blocked by a porous *sieve plate*, as in the *cribri-form* type (Figs 2.11B; 35.18GG, HH). In the last two types, a specialised type of moulting, called by Hinton (1947b) the *elateroid* type, involves the withdrawing of the old tracheal cuticle through an ecdysial tube, which then leaves a scar adjacent to the functional spiracular opening. The entrance chamber or *atrium* of the spiracle may have various kinds of internal armature (Fig. 2.11C). Most beetle spiracles are provided with a spiracular closing apparatus, a device lying between the atrium and tracheal trunk and consisting of an apodeme and muscle capable of closing off the air passage. Among polyphagan larvae, this device is absent in most Scarabaeoidea (except Lucanidae, Passalidae, Trogidae and Glaphyridae) and Elateriformia (except Buprestidae, Eucnemidae, Throscidae, Cerophytidae and Brachypsectridae). The 8th spiracles are often displaced dorsally or located at the ends of single or paired siphon-like tubes in aquatic larvae (e.g. Dytiscidae) or in some terrestrial forms which live in habitats subjected to periodic flooding.

Variations in the abdominal apex include the relative size and position of segment 10 and various modifications of both 9 and 10. T9 often bears a pair of *urogomphi*, which may be fixed (Fig. 35.18N) or articulated (Fig. 35.18J), and occasionally additional armature, while S9 may be armed with single or double rows of asperities (Figs 35.18U, X–Z), which assist in gaining purchase in tight spaces. The entire T9 may form a deciduous lobe (Fig. 35.18P), as in most Scaptiidae, and a movable flap or *operculum* may be dorsally (Fig. 35.18K) or ventrally (Fig. 35.18I) attached to the abdominal apex. In larvae of Lampyridae and many Staphylinidae, segment 10 is provided with a holdfast organ consisting of a number of asperate, eversible tubes (Fig. 35.18CC); in some groups (e.g. Ptilodactylidae) there may be a pair of spinose *pygopods* on the same segment (Figs 35.39E, F), and in others (e.g. Hydraenidae, Ptiliidae, Elmidae) a pair of hooks (Figs 35.18I, J). In Scirtidae, Elmidae (Fig. 35.18I) and Psephenidae, tufts of *anal gills* can be extruded from the abdominal apex, and in most larval Hydrophilidae segments 8 and 9 form a large pocket or *respiratory chamber*, which houses a pair of enlarged 8th spiracles.

**Pupa.** Beetle pupae (Fig. 35.14) are adecticous and nearly always exarate (obtect in Ptiliidae, staphylinine Staphylinidae, Clambidae, Coccinellidae, hispine Chrysomelidae and a few other groups). The abdomen usually includes 9 terga and 8 sterna, and the number of spiracles is usually reduced in comparison with the larva and adult. The head and body often bear various prominences and setae, which serve to hold the pupa away from the walls of the pupal cell. The abdominal apex may have paired appendages similar to larval urogomphi. In a number of groups, including Dermestidae (Fig. 35.14A), there are local sclerotisations on opposable edges of some abdominal segments, which are possibly used to pinch mites and some other predators; these were called *gin traps* by

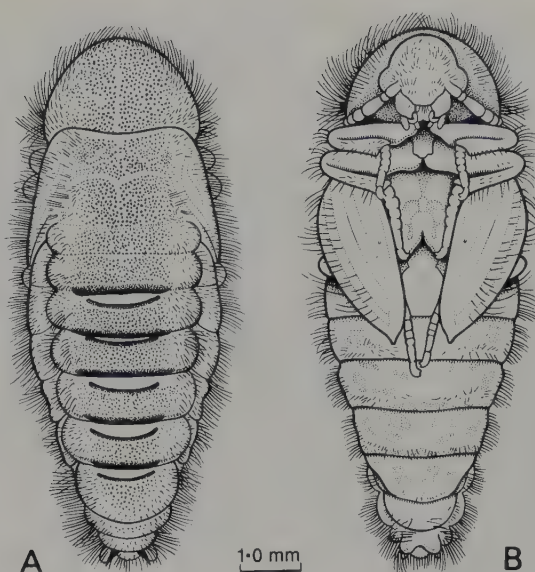


Fig. 35.14 Pupa of *Dermestes maculatus*, Dermestidae: A, dorsal; B, ventral. [F. Nanninga]

Hinton (1946c). In surface-feeding beetles, the pupa often remains partly enclosed by the larval skin, but more commonly pupation occurs within the food plant or in earthen cells below the ground. A cocoon is sometimes constructed. Passalidae and some Scarabaeidae use faecal material, and cryptocephaline Chrysomelidae form a closed capsule from the faecal case of the larva. Silken cocoons are formed by some aleocharine Staphylinidae (Ashe 1982; Frank and Thomas 1984), and have also been reported in several other families (e.g. Brachypsectridae, Bothridiidae, Tenebrionidae, Curculionidae). The calcified remains of certain weevil cocoons (e.g. *Leptopius*) are sometimes found in the soil (Lea 1925).

Further information on immature Coleoptera may be found in Bertrand (1972, 1977; aquatic immatures), Böving and Craighead (1931), Costa *et al.* (1988), Crowson (1981), Marshall *et al.* (in press) and Stehr (1991).

### Biology

**General.** Beetles occupy almost every available terrestrial and freshwater habitat and a few marginal marine habitats as well. They may be found on the foliage of plants of all kinds; in flowers, fruits and seeds; within living plant tissue in galls, stems, branches, trunks and roots; in soil, humus, leaf litter and flood debris; beneath the bark of living and dead trees; in decomposing wood; under stones and logs; in or on the fruiting bodies of various fungi; in dung and carrion; in the nests of vertebrates and social insects; in stored foodstuffs; in fresh water, from temporary pools or billabongs to mountain streams; in the brackish water of salt lakes or estuarine mud flats; in sand, gravel or mud at the edges of streams or ponds; in high-water debris on the seashore; among rocks or coral in the intertidal zone; and in caves.

Members of several beetle families have become adapt-



ed to living in fresh water, either in the larval stage only or throughout the life cycle (except during pupation and adult dispersal). Many adult water beetles (e.g. Hydrophilidae, Elmidae) have on the ventral surface a covering of fine hydrofuge hairs, which serves to trap an air bubble; this is called a *plastron* and has been discussed above (see also Fig. 2.14). Aquatic beetle larvae have evolved a number of respiratory adaptations, including spiracular gills, lateral feathery gills, ventral and anal gill tufts, enlarged terminal spiracles and siphon-like spiracular tubes (see discussions of individual families). Within Australia, all Microsporidae, Haliplidae, Hygrobiidae and Noteridae, almost all Dytiscidae, most Hydrophilidae and Elmidae, and a few Hydraenidae (*Tympanogaster*), Chrysomelidae (*Donacia*) and Curculionoidea are adapted to freshwater existence as both larvae and adults; whereas *Sclerocyphon* (Psephenidae), *Byrrhocryptus* (Ptilodactylidae) and most Scirtidae are aquatic only in the larval stage. Some other groups (e.g. Heteroceridae, the staphylinid genus *Bledius*) live in wet mud or gravel near the water's edge; and *Hyphalus* species (Limnichidae) occur in marine intertidal habitats.

Cave-inhabiting species are less common in Australia than in Europe or North America, but a number of Carabidae belonging to six different tribes have been reported from caves in Tas., Vic., S.A. and Qld, and at least three of them are highly cave-adapted or *troglobitic* (Hamilton-Smith 1967; Moore 1972, unpubl.).

Three somewhat specialised habitats which have been utilised extensively by Coleoptera are the leaf litter and its interface with the soil, decomposing cambium and phloem beneath the bark of dead or dying trees, and mycelial masses or fruiting bodies of various fungi. Each of these habitats is particularly rich in species of Staphyliniformia, Cucujoidea and Tenebrionoidea, and the first two may also be rich in Curculionoidea.

Most species of beetles are phytophagous in the narrow sense, feeding on living plant tissue, but a large number have saprophagous habits and consume only vegetable matter which has been substantially altered by the action of bacteria and fungi. Others are mycophagous (= mycetophagous), specialising in fungal tissue of various kinds. The subject of mycophagy in Coleoptera has been reviewed by Lawrence (1989) and Hammond and Lawrence (1989). The majority of phytophagous beetles belong to the superfamilies Scarabaeoidea, Chrysomeloidea and Curculionoidea, the families Buprestidae, Elateridae, Bostrichidae and Anobiidae, and the coccinellid subfamily Epilachninae.

Carnivorous habits occur in a number of groups, including almost all Adephaga, and a number of polyphagan families, such as Hydrophilidae (larvae), Histeridae, Staphylinidae, Elateridae, Lampyridae, Cantharidae, Cleridae and Coccinellidae. Most of these are general predators on insects and other small invertebrates, but some are limited in their choice of prey. The Coccinellidae, for example, feed largely on aphidoid and coccoid Hemiptera, and Lampyridae usually specialise on snails. Parasitic habits have evolved in a few representatives of the families Carabidae, Staphylinidae, Rhipi-

ceridae, Cucujidae, Bothrideridae, Rhipiphoridae and Meloidae.

**Symbiotic Relationships.** Coleoptera may be involved in a number of symbiotic relationships with other organisms, including endosymbiosis with micro-organisms, ectosymbiosis with certain fungi, ectosymbiosis with mites and nematodes (*phoresy*), and ectosymbiosis with social insects, such as ants, bees and termites (*inquilinism*).

Many beetles harbour aggregations of endosymbionts, which may be extracellular in the lumen of the gut or in various diverticula, or intracellular in the cytoplasm of cells known as *mycetocytes* and sometimes forming special organs called *mycetomes* (A. Koch 1967). Symbionts have been observed most often in species that feed on wood, cereals and other plant material, such as Lucanidae, Passalidae, pleurostict Scarabaeidae, Bostrichidae, Anobiidae, Silvanidae, Tenebrionidae, Cerambycidae, Chrysomelidae and Curculionidae. Mechanisms by which symbionts are transferred to the next generation include 1) entry into newly hatched larvae which consume the contaminated chorion, 2) entry into the egg before secretion of the chorion, and 3) invasion of the testes, passage into the female with the sperm and infection of the egg through the micropyle.

A highly specialised form of ectosymbiosis involves the so-called ambrosia beetles or pinhole borers (family Lymexylidae and weevil subfamilies Scolytinae and Platypodinae) and yeasts of the genera *Ascoidea* and *Endomycopsis*. The beetles bore into wood and, in doing so, introduce these ambrosia fungi which grow on the tunnel walls and serve as food for both larvae and adults. The fungi are always associated with the beetles and are transported from tree to tree by the adult, which often has specialised organs or *mycangia* for the purpose (Francke-Grosmann 1967).

A number of mites and nematodes utilise beetles for transportation from one suitable habitat to another. Examples include saprophagous nematodes of the genus *Goffartia*, which are phoretic on both larvae and adults of Heteroceridae in riparian habitats (Steffan 1967), and a number of mesostigmatid mites (Hunter and Rosario 1988). Members of the mite genus *Macrocheles* are phoretic on dung-feeding Scarabaeidae and predacious on Diptera larvae and other small invertebrates encountered in the dung pads (Krantz 1983).

Beetles in many families have evolved a more or less obligatory relationship with termites or social Hymenoptera, such as ants or bees. These *inquilines* live within the nest for at least part of their life cycle and are usually either tolerated by the host or in some cases protected or even fed by them. Many of the more specialised *inquilines* possess glands of various kinds, which secrete substances imbibed by the host; those which are associated with tufts of hairs are often called *trichomes*. Ant-associated *inquilines* or *myrmecophiles* in the Australian fauna include members of the following families: Carabidae (*Adelotopus*), Ptiliidae (*Rodwayia*), Staphylinidae (various Aleocharinae), Pselaphidae (Clavigerinae), Histeridae (Chlamydopsinae), Dermestidae



(*Myrmeanthrenus*), Anobiidae (ptinine genera *Ectrephes*, *Enasiba*, *Diplocotes* and *Polyplacotes*), Nitidulidae (an undescribed genus), Silvanidae (*Nepharis* and *Nepharinus*), Tenebrionidae (*Euclarkia* and *Kershawia*), Salpingidae (*Tretothorax*) and Brentidae (*Cordus* and *Amorphocephalus*). Some species live in close proximity with ants and may prey on them but do not occur in the nest. Larvae of *Sphallomorpha* (Carabidae: Pseudomorphinae), for instance, live in vertical burrows around the periphery of *Iridomyrmex* nests and feed on worker ants. *Arthropterus* species (Carabidae: Paussinae) are only rarely found in ant nests, but their highly modified antennae and legs suggest that they have evolved protective mechanisms against ant attack; they lack glandular trichomes present in other paussines known to be myrmecophilous.

Australian *termitophiles* occur primarily in the staphylinid subfamily Aleocharinae, where symbiotic associations with termites have evolved a number of times; however they also occur in Ceratocanthidae (*Cyphopisthes*), Scarabaeidae (*Microvalgus*, *Rhyparus*, *Cryptodus*, and *Maechidius* and related melolonthines), Tenebrionidae (*Eutermicola*, *Pseudeba*) and Aderidae (*Megaxenus* with *Microcerotermes*, Lawrence *et al.* 1990). The aleocharine *Austrospirachtha mimetes*, which lives in *Nasutitermes* colonies, is capable of expanding the abdomen so that it takes on the appearance of a termite worker (Figs 35.27F, G) (Watson 1973). The highly specialised larvae of *Drepanoxenus* (Fig. 35.27E) species, which live in the nests of harvester termites (*Drepanotermes*), have reduced, suctorial mouth-parts, long geniculate antennae, and lateral intersegmental glands on the thorax and abdomen. These larvae are treated as colony members and are groomed by the termite workers, which appear to gain some benefit from the glandular secretions (Kistner and Watson 1972; Watson and Kistner 1972). Other Australian termitophilous Aleocharinae include members of the genera *Australoptochus*, *Lauiella*, *Austrointhus*, *Microceroxenus*, *Nasutiphilus*, *Coptotermoeia*, *Philobrunneus*, *Hetairotermes*, *Termitoecia* and *Mastopsenius*.

**Defensive Adaptations.** In Coleoptera, defence against attack by bacteria and fungi, as well as predators, is commonly achieved by means of chemical compounds secreted by special glands on various parts of the body, or sometimes located in the haemolymph and released by *reflex bleeding* or crushing of the cuticle. The subject of defence chemistry in beetles has been reviewed by Dettner (1987) and discussed in general texts (Crowson 1981). Chemical defence mechanisms have evolved at least 30 times in the order, and have been demonstrated in various groups, including all Adephaga and various members of the families Histeridae, Silphidae, Staphylinidae, Scarabaeidae, Buprestidae, Elateridae, Cantharidae, Lampyridae, Lycidae, Trogossitidae, Melyridae, Endomychidae, Coccinellidae, Meloidae, Oedemeridae, Pyrochroidae, Pythidae, Tenebrionidae, Cerambycidae and Chrysomelidae. Glands are often located at or near the abdominal apex, with their reservoirs opening in the membrane between apical or subapical tergites or stern-

ites; the *pygidial glands* of Adephaga are of this type, as are those of Tenebrionidae, Scarabaeidae and some Staphylinidae. In other groups the glands may be generally distributed on the dorsal surfaces of the pronotum and elytra (chrysomeline, criocerine and galerucine Chrysomelidae) (Deroe and Pasteels 1982), near the anterior edge of the prothorax (some Dytiscidae and Tenebrionidae), or on most abdominal segments (larvae and adults of Cantharidae). Larvae of *Paropsis* and related Chrysomelidae secrete a lethal mixture containing hydrogen cyanide stored in eversible vesicles on T8 (B. P. Moore 1967). Hinton (1951) showed that glandular reservoirs present in some chrysomeline larvae were utilised by the pupae as well, since the latter remain partly enclosed within the larval skin. Lawrence and Hlavac (1979) suggested that the complex cuticular topography (canals, basins, pores and bridges) exhibited by adults of some Derodontidae, Hydraenidae, Hydrophilidae, Micropeplidae, Pselaphidae, Colydiidae and Tenebrionidae may function as a drainage and containment system for defensive chemicals. Many distasteful or poisonous species are *aposematically* coloured and belong to mimetic assemblages discussed by Moore and Brown (1989).

Among the non-chemical types of defence are the specialised hairs (spicisetae and hastisetae) found in the larvae of most Dermestidae. These hairs are easily detached and adhere to the appendages of ants and other predators, thereby neutralising their attack (Nutting and Spangler 1969). Faeces and other debris which adhere to the cast skins impaled on the long fork arising from T8 in tortoise beetle larvae (Chrysomelidae: Hispinae) have been observed to discourage predators (Eisner *et al.* 1967).

**Reproduction and Life History.** The antennae of male Coleoptera are often larger and more elaborate than those of females; this is presumably correlated with the emission of pheromones by the female, which stimulate the male to fly upwind in search of a mate. Glandular setose areas (*sex patches*) occur on various parts of the body (e.g. frons, mentum, prosternum, abdomen, legs) in males only or less often in both sexes; at least some of these are known to produce aggregation pheromones, which attract both sexes (Faustini and Halstead 1982; B. A. Holloway 1985; W. W. K. Houston 1986).

In some groups (e.g. Scarabaeidae, Ciidae, Tenebrionidae), males have horns on the head and/or pronotum, which exhibit allometric variation and are used in combat with males of the same species (Eberhard 1979, 1980, 1982; Cook 1987). Complex courtship behaviour preceding copulation has been reported for a number of families, including Melyridae, Meloidae and Cerambycidae (Crowson 1981). In copulation, the male usually assumes a position on the back of the female, sometimes using modified fore or mid tibiae or tarsi to stay in position. The necessity to curve the abdomen down and forwards to reach the apex of the female's abdomen is often obviated by a curvature in the penis; the latter is inserted into the vagina, with the internal sac being everted subsequently into the female tract.

The number of eggs deposited varies greatly through-



out the order. Minute beetles (e.g. Microsporidae and Ptiliidae) produce only 1 or 2 eggs at a time, while very large numbers of small eggs may be found in the abdomens of some Lymexylidae and Meloidae. *Oothecae* or cases enclosing a number of eggs occur in various Chrysomelidae (e.g. Sagrinae, Cryptocephalinae, Eumolpinae, Hispinae) and some other groups. Subsocial behaviour, i.e. parental care of eggs or larvae, is known in at least 10 beetle families (Eickwort 1981; Wilson 1971). In *Spercheus* (Hydrophilidae), eggs are carried beneath the abdomen of the female until hatching, and some Carabidae and Staphylinidae place the eggs in a special chamber, which is defended. Females of *Bledius* (Staphylinidae) maintain and defend the larval tunnels and provide algal food, while some harpaline Carabidae store seeds for their larvae. Males and females of Geotrupidae and scarabaeine Scarabaeidae often co-operate in digging nests and providing the larvae with plant material or dung, and progressive provisioning during the life of the larvae occurs in the latter group and also in silphid beetles of the genus *Nicrophorus*. Some degree of subsociality also occurs in gregarious wood-feeding Passalidae (Reyes-Castillo and Halffter 1983), in the tenebrionid genus *Phrenapates*, and in some ambrosia beetles (scolytine and platypodine Curculionidae).

Unusual life cycles have evolved in various families. *Ovoviviparity*, in which the eggs are retained in the female reproductive tract until hatching, is known in some aleocharine Staphylinidae, chrysomeline Chrysomelidae, Tenebrionidae and pseudomorphine Carabidae (Liebherr and Kavanaugh 1985). Larval *heteromorphosis* or *hypermetamorphosis*, usually involving an active 1st instar or *triungulin* and grub-like, inactive, sometimes legless, later instars, occurs in several groups of parasitoids (e.g. lebiine Carabidae, some aleocharine Staphylinidae, Rhipiceridae, passandrine Cucujidae, bothriderine Bothrideridae, Rhipiphoridae and Meloidae), but similar phenomena are also known in some wood-boring groups (Micromalthidae, Lymexylidae, Bostrichidae). Various Coleoptera may have distinctive 1st instars or pre-pupal resting stages (*prepupae*). *Paedogenesis* or the retention of larval features in adult females occurs in Micromalthidae, Phengodidae and the Asian lycid genus *Duliticola*; the pupal stage is eliminated and the females are indistinguishable from larvae, except for the reproductive organs. In other groups, such as Dascillidae (Karumiinae), Elateridae (Cebrioninae), Drilidae, Lampyridae, Dermestidae (*Thylodrias*) and Rhipiphoridae (Rhipidiinae), the females lack hind wings and often elytra but have adult legs, antennae and mouth-parts.

*Parthenogenesis* is relatively uncommon in beetles, but it occurs in a number of weevils (e.g. *Otiorhynchus*), and in some other families, such as Chrysomelidae, Ptiliidae, Ciidae and Bothrideridae (*Anommatus*). Pseudogamous parthenogenesis occurs in the triploid form of *Ptinus clavipes*; these females reproduce only after mating with males of *P. clavipes*, *P. pusillus* or *P. fur*, and the offspring are all females of the form *mobilis* (Woodroffe 1958).

**Natural Enemies.** Coleoptera are subject to attack by

the usual array of predators, parasitoids and diseases. Eggs may be attacked by various Hymenoptera (e.g. Mymaridae, Pteromalidae) and larvae are preyed upon by spiders, wasps (e.g. *Cerceris*), other beetles and vertebrates, and parasitised by Chalcidoidea (HYMN), Braconidae (HYMN), Ichneumonidae (HYMN) and Tachinidae (DIPT). Larvae living in the soil are attacked by mites and nematodes. Tiphid wasps of the subfamily Thynninae and the large rutiline Tachinidae are common parasitoids of soil-dwelling scarabaeid larvae in Australia, and members of the Pyrgotidae (DIPT) and some Braconidae parasitise adult beetles. Aquatic beetles form an appreciable part of the food of fish, and most amphibians and many reptiles and birds feed to a large extent on beetles and other insects. Coleoptera are also subject to various diseases caused by fungi, bacteria and viruses.

**Economic Significance.** The economic importance of Coleoptera results mostly from the damage some species inflict on materials of value to man, such as agricultural crops, pasture plants, timber resources, and stored products, and the activities of other species in controlling insect or plant pests. They are of little or no importance in the transmission of diseases to man or other mammals and only a few transmit plant diseases or cause dermatitis (see below). Pasture plants, cereal crops and sugar cane are most seriously affected by soil-dwelling, root-feeding larvae of Scarabaeidae (whitegrubs, canegrubs, cockchafers, e.g. *Adoryphorus couloni*, *Lepidiota* spp., *Rhopaea* spp., *Sericesthis* spp., *Heteronychus arator*, *Aphodius tasmaniae*), Elateridae (wireworms, e.g. *Agrypnus* spp. and *Conoderus* spp.) and Tenebrionidae (false wireworms, e.g. *Gonocephalum* spp. and *Pterohelaenus* spp.). Cucurbits may be damaged by species of *Aulacophora* (Chrysomelidae) and *Epilachna* (Coccinellidae). *Cosmopolites sordidus* is a serious pest of bananas, and a variety of fruit trees and garden crops are attacked by introduced weevils (e.g. *Asynonychus cervinus*, *Graphognathus leucoloma*, *Listroderes difficilis*, *Otiorhynchus* spp., *Phlyctinus callosus*). Some Cerambycidae, such as *Uracanthus cryptophagus*, attack the wood of fruit trees, while others (e.g. *Zygrita* and *Corrhenes*) damage soybean and lucerne. The wood of native timber or shade trees is subject to attack by various Cerambycidae (e.g. *Phoracantha*), and their foliage is sometimes severely reduced by Chrysomelidae (*Paropsis* and related genera), Scarabaeidae (adult *Anoplognathus*) or Curculionidae (*Goniapterus*). Also, ambrosia beetles (e.g. *Platypus* and *Xyleborus*) cause blue staining of timber, and *Platypus subgranosus* carries a fungal pathogen fatal to Tasmanian rainforest trees (Elliot and De Little 1985). A potentially serious future threat is posed by the introduced bark beetle *Ips grandicollis*, which attacks *Pinus radiata* plantations (Morgan 1967).

Stored products attacked by beetles include a variety of foodstuffs, leather goods, wood, tobacco and crude drugs. Pests of stored products tend to be adapted to dry environments, and some of them, such as the anobiids *Stegobium paniceum* and *Ptinus tectus*, are capable of breeding in a wide variety of materials, while others may be more restricted in their food requirements (e.g.



*Dermestes* species which attack dry animal material of high protein content, and *Sitophilus* species which infest whole grains of wheat, rice, barley or maize). A number of Tenebrionidae occur in stored grains and cereal products, whereas wooden articles are often attacked by Anobiidae or Bostrichidae. About 400 beetle species have been reported from stored products, but only a small proportion of these feed directly on the stored material; some are mycophagous, some predacious, and others of accidental occurrence. Information on stored products beetles may be found in Aitken (1975), Freeman (1980), Hinton (1945a) and Lepesme (1944).

Coleoptera have played an important part in the biological control of insect pests and noxious plant species. Various Coccinellidae have been used to control plant pests belonging to the Aphidoidea and Coccoidea (HEMI). Some Australian species (e.g. *Rodolia cardinalis*, *Cryptolaemus montrouzieri* and *Rhyzobius* spp.) have been imported into the United States for the control of certain scale insects and mealybugs (HEMI) (p. 232). Exotic beetles have also been imported into Australia to control introduced insect pests, a recent example being *Trogossita virescens* (Trogossitidae) and *Thanasimus formicarius* (Cleridae), imported from the Northern Hemisphere for the control of *Ips grandicollis*. Other importations have involved the control of noxious plants. The classic example is the introduction of the European chrysomelids *Chrysolina hyperici* and *C. quadrigemina* for the control of St John's wort (*Hypericum perforatum*). Other notable examples of biological control agents and their hosts are as follows (Chrysomelidae, except where noted): *Octotoma* and *Uroplata* for *Lantana camara*; *Moneilema* (Cerambycidae) for *Opuntia* (prickly pear); *Cyrtobagous salviniae* (Curculionidae) for *Salvinia molesta*; *Longitarsus jacobaeae* for *Senecio jacobaea* (ragwort); *Agasicles hygrophila* for *Alternanthera philoxeroides* (alligator weed); and *Acanthoscelides* and *Chlamisus* for *Mimosa pigra* (giant sensitive plant) (Harley *et al.* 1985; Julien 1987). Coprophagous Coleoptera (*Geotrupes* and scarabaeine Scarabaeidae) have been imported from South Africa and the Mediterranean Region for the control of cattle dung and dung-breeding flies (Bornemissza 1976; Waterhouse 1974).

Species of *Paederus* (Staphylinidae) cause severe skin lesions, often referred to as whip-lash dermatitis, when the adult beetles land on humans and are crushed when swatted or brushed, causing an irritating compound, pederin, to be released onto the skin (Frank and Kanamitsu 1987; Whelan and Weir 1987). Similar reactions may be caused by another chemical, cantharidin, produced by beetles of the families Meloidae and Oedemeridae (Moore and Brown 1989).

### Special Features of the Australian Fauna

Of the more than 500 generally recognised families and subfamilies of Coleoptera, about two-thirds are represented in Australia, and these include all of the larger and better known taxa. Among the large, dominant groups that have radiated extensively during the latter part of the

Tertiary in association with *Eucalyptus* and *Acacia* communities are the scaritine Carabidae, bolboceratine Geotrupidae, anoplognathine Rutelinae and heteronychine and liparetrine Melolonthinae (Scarabaeidae), stigmoderine Buprestidae, agrypnine Elateridae, anthrenine Dermestidae, malachiine Melyridae, adeline and heleine Tenebrionidae, phoracanthine Cerambycidae, cryptocephaline, eumolpine and chrysomeline Chrysomelidae, and amycerine and leptopiine Curculionidae.

The degree of endemism is very high, and endemic taxa include three families (Rhinohipidae, Acanthocnemidae and Lamingtoniidae), several subfamilies and numerous tribes and genera. A few taxa, which are relatively common in most parts of the world, are either absent in Australia or represented by a small number of native species; these include brachinine Carabidae (1), geotrupine Geotrupidae (0), Dryopidae (0), Lampyridae (25), meligethine Nitidulidae (1), Tetratomidae (0), eustrophine Melandryidae (0), pimeline Tenebrionidae (3), Meloidae (60), bruchine Chrysomelidae (20) and lepturine Cerambycidae (0). A few families, such as Dryopidae and Pterogeniidae, occur in New Guinea and may be found eventually in northern Australia.

Modern Indo-Malayan (or Torresian) elements in the fauna are common, especially in the rainforests of northern Qld; included are such genera as *Tricondyla* (Carabidae: Cicindelinae), *Omicrini* (Hydrophilidae), *Priochirus* (Staphylinidae: Osoriinae), *Trypeticus* (Histeridae), *Xylotrupes* and *Haploscapanes* (Scarabaeidae: Dynastinae), *Cyphogastra* and *Iridotaenia* (Buprestidae), *Pseudeucinetus* (Limnichidae), *Melanotus* and *Cussolenis* (Elateridae), *Pteroptyx* (Lampyridae), *Sarothrias* (Jacobsoniidae), *Encaustes* and *Aulacochilus* (Erotylidae), *Chariotheca* and *Promethis* (Tenebrionidae), *Horia* (Meloidae), *Batocera* (Cerambycidae), *Sagra* and *Donacia* (Chrysomelidae), *Ithysten* (Brentidae) and *Baris*, *Mecopus* and *Sipalinus* (Curculionidae).

Like most groups of Australian organisms, Coleoptera provide numerous examples of South Temperate or Gondwanan relationships. Some of these taxa display a typical southern or Bassian distribution within Australia, while others are widespread on the continent or restricted to tropical mountains in northern Qld. Most of these Gondwanan groups have representatives in New Zealand and sometimes New Caledonia as well; examples include Pamborini (Carabidae), Trichelodini (Dermestidae), Phycosecidae, Priasilphinae (Phloeostichidae), and the tenebrionid tribes Zolodini, Heleini and Titaenini. Other groups have representatives in both New Zealand and South America; these include Migadopini and Zolini (Carabidae), Camiarinae (Leiodidae), Microsilphini and Comeolabiini (Staphylinidae: Omaliinae), *Ceratognathus* and Lampriminae (Lucanidae), *Nothoderodontus* (Derodontidae), Rentoniinae (Trogossitidae), Cavognathidae, Ulodinae (Zopheridae), Adeliini (Tenebrionidae), Lagriodinae (Anthicidae), Belidae and Phrynixini (Curculionidae). Some taxa have their closest relatives in South America but lack New Zealand representatives; among these are *Cochliarion* (Ptiliidae), *Neopelatops* (Leiodidae), *Glypholoma* (Staphylinidae), *Syndesus* and

*Sphaenognathus* (Lucanidae), Aclopinæ (Scarabaeidae), Egoiinae (Trogossitidae), Protocucujidae, Hymæinae (Phloeostichidae) and Hobartiidae.

Another set of Australian taxa belong to amphipolar groups (Crowson 1980; amphitropical groups of Darlington 1965), which have both North Temperate and South Temperate members. Among these are the Byrrhidae and Pilipalpinae (Pythidae), which also have representatives in South Africa or Madagascar; Broscini

(Carabidae) and Nemonychidae, which are absent from Africa and Madagascar; and Dacoderinae (Salpingidae) and Pythinae (Pythidae), which occur only in Australia and the Holarctic Region. An unusual pattern may be seen in the Boganiidae, both subfamilies of which occur in Australia and South Africa. H. F. Howden (1981) discussed the zoogeography of some Australian Coleoptera, and further examples of South Temperate distributions are given by Newton (1985).

## CLASSIFICATION

### Order COLEOPTERA (28 200)\*

#### Suborder ARCHOSTEMATA (9)

##### CUPEDOIDEA (9)

##### 1. Ommatidae (3)

##### 2. Cupedidae (6)

##### Micromalthidae (0)

#### Suborder MYXOPHAGA (2)

##### MICROSPOROIDEA (2)

##### Torridincolidae (0)

##### Cyathoceridae (0)

##### Hydroscephidae (0)

##### 3. Microsporidae (2)

#### Suborder ADEPHAGA (2730)

##### CARABOIDEA (2730)

##### Trachypachidae (0)

##### 4. Rhysodidae (8)

##### 5. Carabidae (2500)

##### 6. Haliplidae (5)

##### 7. Hygrobiidae (3)

##### Amphizoidae (0)

##### 8. Noteridae (5)

##### 9. Dytiscidae (185)

##### 10. Gyrinidae (25)

#### Suborder POLYPHAGA (25 450)

##### *Staphyliniformia*

##### HYDROPHILOIDEA (360)

##### 11. Hydrophilidae (175)

##### Sphaeritidae (0)

##### Synteliidae (0)

##### 12. Histeridae (185)

##### STAPHYLINOIDEA (2670)

##### 13. Hydraenidae (55)

##### 14. Ptiliidae (75)

##### Agyrtidae (0)

##### 15. Leiodidae (135)

##### 16. Scydmaenidae (300)

##### 17. Silphidae (3)

##### Micropeplidae (0)

##### Dasycteridae (0)

##### 18. Staphylinidae (1600)

##### 19. Pselaphidae (900)

##### 27. Ceratocanthidae (2)

##### 28. Hybosoridae (40)

##### Glaphyridae (0)

##### 29. Scarabaeidae (3000)

##### *Elateriformia*

##### DASCILLOIDEA (15)

##### 30. Dascillidae (2)

##### 31. Rhipiceridae (13)

##### BUPRESTOIDEA (1200)

##### 32. Buprestidae (1200)

##### BYRRHOIDEA (276)

##### 33. Byrrhidae (40)

##### Dryopidae (0)\*\*

##### Lutrochidae (0)

##### 34. Elmidae (150)

##### 35. Limnichidae (30)

##### 36. Heteroceridae (15)

##### 37. Psephenidae (15)

##### 38. Callirhipidae (10)

##### Eulichadidae (0)

##### 39. Ptilodactylidae (15)

##### 40. Chelonariidae (1)

##### Cneoglossidae (0)

##### ELATEROIDEA (1380)

##### Artematopidae (0)

##### 41. Rhinorhipidae (1)

##### 42. Brachypsectridae (1)

##### Cerophytidae (0)

##### 43. Eucnemidae (160)

##### 44. Throscidae (20)

##### 45. Elateridae (800)

##### Plastoceridae (0)

##### Drilidae (0)

##### Homalidae (0)

##### 46. Lycidae (240)

##### Telegeusidae (0)

##### Phengodidae (0)

##### 47. Lampyridae (25)

##### Omethidae (0)

##### 48. Cantharidae (150)

##### *Bostrichiformia*

##### DERODONTOIDEA (1)

##### 49. Derodontidae (1)

##### BOSTRICHOIDEA (440)

##### 50. Jacobsoniidae (5)

##### 51. Nosodendridae (3)

##### 52. Dermestidae (150)

##### Endecatomidae (0)

##### 53. Bostrichidae (60)

##### 54. Anobiidae (225)

##### *Cucujiformia*

##### LYMEXYLOIDEA (10)

##### 55. Lymexylidae (10)

##### CLEROIDEA (700)

##### Phloiophilidae (0)

##### 56. Trogossitidae (40)

##### Chaetosomatidae (0)

##### 57. Cleridae (350)

##### 58. Acanthocnemidae (1)

##### 59. Phycosecidae (3)

##### 60. Melyridae (300)

##### CUCUJOIDEA (1300)

##### 61. Protocucujidae (4)

##### 62. Sphindidae (8)

##### 63. Nitidulidae (300)

##### *Eucinetiformia*

##### EUCINETOIDEA (100)

##### 20. Scirtidae (70)

##### 21. Eucinetidae (10)

##### 22. Clambidae (20)

##### *Scarabaeiformia*

##### SCARABAEOIDEA (3560)

##### 23. Lucanidae (85)

##### 24. Passalidae (40)

##### 25. Trogidae (50)

##### Glaresidae (0)

##### Pleocomidae (0)

##### Diphyllostomatidae (0)

##### 26. Geotrupidae (140)

##### Ochodaeidae (0)



64. Rhizophagidae (12)	TENEBRIONOIDEA (2600)	Pedilidae (0)
65. Boganiidae (13)	86. Mycetophagidae (10)	Pyrochroidae (0)
Helotidae (0)	87. Archeocrypticidae (20)	102. Salpingidae (30)
66. Phloeostichidae (12)	Pterogeniidae (0)**	103. Anthicidae (200)
67. Silvanidae (60)	88. Ciidae (120)	104. Aderidae (100)
68. Cucujidae (15)	Tetratomidae (0)	105. Scaptidae (25)
69. Laemophloeidae (50)	89. Melandryidae (50)	CHRYSMELOIDEA (4200)
70. Propalticidae (3)	90. Mordellidae (120)	Vesperidae (0)
71. Phalacridae (100)	91. Rhipiphoridae (60)	Anoplodermatidae (0)
72. Hobartiidae (2)	92. Colydiidae (120)	Oxypeltidae (0)
73. Cavognathidae (3)	93. Monommidae (1)	Disteniidae (0)
74. Cryptophagidae (50)	94. Zopheridae (50)	106. Cerambycidae (1200)
75. Lamingtoniidae (1)	Perimylopidae (0)	107. Chrysomelidae (3000)
76. Languriidae (30)	95. Chalcodryidae (2)	CURCULIONOIDEA (6640)
77. Erotylidae (50)	Trachelostenidae (0)	108. Nemomychidae (15)
78. Biphyllidae (35)	96. Tenebrionidae (1500)	109. Anthribidae (150)
Byturidae (0)	97. Prostomidae (6)	Urodontidae (0)
79. Bothrideridae (40)	Synchroidea (0)	Oxycorynidae (0)
80. Cerylonidae (40)	98. Oedemeridae (85)	Allocorynidae (0)
81. Discolomidae (15)	Cephaloidae (0)	Aglycyderidae (0)
82. Endomychidae (50)	99. Meloidae (60)	110. Belidae (175)
Alexiidae (0)	100. Mycteridae (20)	111. Attelabidae (100)
83. Coccinellidae (300)	Boridae (0)	Ithyceridae (0)
84. Corylophidae (60)	Tricentenotomidae (0)	112. Brentidae (200)
85. Lathridiidae (55)	101. Pythidae (20)	113. Curculionidae (6000)

\* Numbers in brackets are the approximate numbers of species known in collections (but not necessarily described).

\*\* Occurring in New Guinea.

Of the several major classifications of Coleoptera which claim to reflect the phylogeny of the order, the most recent and widely accepted is that of R. A. Crowson, first published in its entirety in 1955 and variously modified in later papers (Crowson 1960, 1967, 1971a, 1971b, 1973b). A comparison of his classification with those of Ganglbauer (1903), Lameere (1903), Kolbe (1908) and Peyerimhoff (1933) (see Crowson 1971b) shows that he incorporated many of the features of previous systems (especially that of Peyerimhoff, who, like Crowson, was strongly influenced by the larval work of Böving and Craighead 1931) but made a number of significant innovations. These include the following: (1) recognition of a fourth suborder, Myxophaga, for a few small families of aquatic beetles (see p. 612); (2) rejection of the concept of Haplogastra/Symphioastra, in which the Polyphaga are divided into two groups based on the loss of the 2nd abdominal sternite (see Jeannel and Paulian 1944); (3) placement of the Staphylinioidea, Histeroidea and Hydrophiloidea in a series Staphyliniformia, and treatment of the last two as independent superfamilies; (4) formation of a series Eucinetiformia for the primitive families Eucinetidae, Clambidae and Scirtidae; (5) incorporation of the Dascillidae and Rhipiceridae into a superfamily Dascilloidea, considered to be the sister group of the Scarabaeoidea (series Scarabaeiformia); (6) combining the Byrrhoidea, Dryopoidea, Buprestoidea,

Elateroidea and Cantharoidea into a series Elateriformia, together with elements formerly included in Dascilloidea; (7) inclusion of Dermestidae, Bostrichoidea and a few isolated groups (Derodontidae, Nosodendridae and Jacobsoniidae) into a series Bostrichiformia; and (8) inclusion of the order Strepsiptera (as Stylopoidea) in the most derived series, Cucujiformia, along with the Lymexylidae, Cleroidea, Clavicornia (Cucujoidea), Heteromera, Phytophaga (Chrysomeloidea) and Rhynchophora (Curculionoidea) of older systems.

Lawrence and Newton (1982) criticised concepts 5, 7 and 8, and suggested alternate family placements in Staphyliniformia and Elateriformia. Lawrence (1988b) suggested further family alignments within an expanded Elateriformia (including Dascilloidea), but not all of these are followed here (see pp. 643–6). The following treatment differs from that of Crowson mainly in the inclusion of Histeridae and related families in the Hydrophiloidea; the incorporation of Hydraenidae into Staphylinioidea; the inclusion of Dascilloidea in Elateriformia; the inclusion of the dryopoid families and Byrrhidae in Byrrhoidea; the uniting of Armatopidae, Elateroidea and Cantharoidea into one superfamily; the placement of Jacobsoniidae, Nosodendridae and Dermestidae in Bostrichoidea; the separation of Tenebrionoidea (Heteromera) from Cucujoidea (Clavicornia); and the removal of Strepsiptera from the order (see Chapters 5, 6 and 36).

#### *Keys to the Families of Coleoptera Known in Australia*

##### ADULTS (Larval key on p. 588)

1. Prothorax with pair of notopleural sutures (distinct from sharp lateral margins) separating notum from externally visible pleuron on each side (Figs 35.3A, B) (pleura may or may not be separated from sternum by additional pair of pleurosternal sutures); tarsi always 5-segmented, antennae never with 3-segmented club, and body length always greater than 1 mm ..... (ARCHOSTEMATA and ADEPHAGA) 2



Fig. 35.15 Illustrations for adult key. A-F, heads, dorsal or anterodorsal: A, *Meneristes intermedius*, Tenebrionidae; B, *Chauliognathus apterus*, Cantharidae; C, *Metriorrhynchus rufipennis*, Lycidae; D, *Luciola olivieri*, Lampyridae; E, *Aspidiphorus* sp., Sphindidae, right mandible spread; F, *Microchaetes* sp., Byrrhidae, showing occipital ridge. G, *Pseudomicrocara* sp., Scirtidae, head, ventrolateral, showing genal ridges. H, *Ptilodactyla* sp., Ptilodactylidae, prothorax, right lateral. I-S, prothoraces, ventral: I, *Peltonyxa* sp., Trogossitidae; J, *Byrrhoeus variegatus*, Ptilodactylidae; K, *Acanthocnemus nigricans*, Acanthocnemidae; L, *Melittomma* sp., Lymexylidae; M, *Priastichus tasmanicus*, Phloeostichidae; N, *Conoderus* sp., Elateridae; O, *Loboglossa* sp., Mycteridae; P, *Syndesus cornutus*, Lucanidae; Q, *Scymena variabilis*, Tenebrionidae; R, *Austronabis* sp., Silvanidae; S, *Meryx rugosa*, Zopheridae. T-W, pterothoraces, ventral: T, *Morpholycus costipennis*, Pythidae; U, *Nascioides parryi*, Buprestidae; V, *Melittomma* sp., Lymexylidae; W, *Omorgus candidus*, Trogidae. X, *Eurhynchus laevior*, Brentidae, prothorax, left ventrolateral. Y-AA, tarsi: Y, *Ennometes* sp., Callirhipidae; Z, *Notodascillus* sp., Dascillidae; AA, *Ecnolagria grandis*, Tenebrionidae. BB, *Australiorylon longipilis*, Cerylonidae, abdominal apex, ventral.

[S. Smith]



- Prothorax without notopleural sutures, ventral portion of notum (hypomeron) on each side joined directly to sternum by notosternal suture and pleuron reduced and concealed (Figs 35.3c, 15H–S) (except in *Microspor*, where tarsi are 3-segmented, antennae have 3-segmented club and body length is less than 1 mm) ..... (MYXOPHAGA and POLYPHAGA) 10
- 2(1). Abdomen with 6 ventrites, first 3 of which fused and first of which divided into 2 or 3 parts by hind coxae (Figs 35.3A, 6A); usually either aquatic species with streamlined form and swimming hairs on at least one pair of legs or terrestrial ones with antenna cleaner on fore tibia (Fig. 35.4A) ..... 3
- Abdomen with 5 free ventrites, first of which is entire; terrestrial species without antenna cleaner on fore tibia ..... 9
- 3(2). Hind coxae not extending laterally to meet elytra, so that junction of metepimeron and first ventrite usually visible (Fig. 35.6A); antennae largely pubescent; dorsal surfaces with well-developed, erect, sensory setae at fixed positions (Fig. 35.21G) ..... 4
- Hind coxae extending laterally to meet elytra, so that junction of metepimera and first ventrite is not visible (Figs 35.22D, F); antennae entirely or almost entirely glabrous; dorsal surfaces rarely with erect, fixed sensory setae ..... 5
- 4(3). Transverse metasternal suture absent; hind coxae widely separated, so that large mesal portion of first ventrite visible between them; antennae relatively thick and moniliform (Fig. 35.21A); head, pronotum and sometimes elytra with deep longitudinal grooves, often lined with micropapillae (appearing as dull greyish surface) ..... **Rhysodidae** (p. 609)
- Transverse metasternal suture present (Fig. 35.6A); hind coxae contiguous or only moderately separated, so that mesal exposed portion of first ventrite is very small or absent; antennae slender and filiform (rarely short and clavate or with expanded and flattened segments); without deep furrows on head and pronotum ..... **Carabidae** (p. 611)
- 5(3). Hind coxae with very large plates concealing basal ventrite and most of hind femora (Fig. 35.22B); metasternum with distinct transverse suture; elytra with large punctures forming regular rows ..... **Haliplidae** (p. 614)
- Hind coxal plates absent or consisting of narrow mesal portion only, not concealing basal ventrites or femora; if metasternal suture present, then elytra without regular puncture rows ..... 6
- 6(5). Metasternum with transverse suture (Fig. 35.22D); head more exerted, eyes protuberant and well separated from anterior edge of prothorax (Fig. 35.22C); hind coxae relatively small, their lateral portions shorter than metasternum ..... **Hygrobiidae** (p. 614)
- Metasternum without transverse suture; head less exerted, eyes not protuberant and usually in contact with anterior edge of pronotum; hind coxae much larger, their lateral portions longer than metasternum (Fig. 35.22F) ..... 7
- 7(6). Eyes completely divided into dorsal and ventral portions; antennae very short and thick, with a very large pedicel; elytra truncate exposing most of one abdominal tergite; fore legs long and raptorial, mid and hind legs short and paddle-like (Fig. 35.22I) ..... **Gyrinidae** (p. 616)
- Eyes not completely divided; antennae longer, without enlarged pedicel; elytra concealing abdominal tergites; fore legs not long and raptorial, mid and hind legs longer and narrower ..... 8
- 8(7). Dorsal surface strongly convex; scutellum not visible (Fig. 35.22E); ventral surface flattened; hind coxae with characteristic longitudinal plates covering bases of trochanters (Fig. 35.22F); junction between metasternum and hind coxae angulate in middle; metepisterna clearly not reaching mid coxal cavities ..... **Noteridae** (p. 615)
- Dorsal surface hardly more convex than ventral surface; scutellum sometimes visible; hind coxae without plates; junction of metasternum and hind coxae arcuate; metepisterna reaching or almost reaching mid coxal cavities ..... **Dytiscidae** (p. 616)
- 9(2). Antennal insertions dorsal and more or less approximate; antennae longer than head and prothorax together (Fig. 35.19B); labrum free and visible; fore coxal cavities separated by prosternal process; tarsal segment 4 lobed beneath; ventral surfaces of prothorax and pterothorax with distinct grooves for reception of legs (Fig. 35.19C) ..... **Cupedidae** (p. 607)
- Antennal insertions lateral, well separated; antennae shorter than head and prothorax together (Fig. 35.19A); labrum not distinct; fore coxal cavities contiguous; tarsal segment 4 not lobed; ventral surfaces without grooves for reception of legs ..... **Ommatidae** (p. 607)
- 10(1). Antennae with a 3- to 8-segmented, strongly asymmetrical club, which is usually lamellate (Figs 35.29A, E, F, 31A, 32); head visible from above, not covered by prothorax; fore coxae very large, strongly transverse or conical and projecting below prosternum, with concealed trochantins and posteriorly closed cavities (Fig. 35.15P); fore tibiae usually flattened with one or more teeth on outer edge (Figs 35.29A, B, E, F, 31A–C, 32, 33A); tarsi with 5 distinct segments, none of which is lobed or densely pubescent ..... (SCARABAEOIDEA) 11
- Antennae rarely with strongly asymmetrical or lamellate club; if so, then club with more than 8 segments, fore coxae smaller with exposed trochantins, fore coxal cavities open behind, head concealed from above by prothorax or fore tibiae and tarsi different ..... 17
- 11(10). Antennal segments 11; antennal club circular or oval, cupuliform; body highly convex and hemispherical, often with extensive armature on head and prothorax (Fig. 35.29A) ..... **Geotrupidae** (p. 627)
- Antennal segments fewer than 11 ..... 12
- 12(11). Mid coxal cavities open laterally (partly closed by mesepimera) (Figs 35.15T, U) ..... 13
- Mid coxal cavities closed laterally by broad meeting of meso- and metasterna (Fig. 35.15W) ..... 16
- 13(12). Body strongly contractile, capable of being rolled into the shape of a ball (Fig. 35.29C); eye completely divided into

- two parts by an ocular canthus; hind tibiae and to a lesser extent fore and mid tibiae expanded and flattened, with a carinate outer edge; body length less than 5 mm ..... **Ceratocanthidae** (p. 627)
- Body not contractile, or if moderately so, then eye not completely divided, hind tibiae not flattened and carinate and body length more than 5 mm ..... 14
- 14(13). Segments of antennal club relatively thick and not capable of close apposition (Fig. 35.29E); abdomen with 5 ventrites; males with enlarged mandibles but only rarely with tubercles or horns on head or pronotum ..... **Lucanidae** (p. 625)
- Segments of antennal club usually thin and always capable of close apposition (Figs 35.32, 33A); abdomen with 6 ventrites; mandibles in male not larger than those in female, male armature (if present) involving head and/or prothorax ..... 15
- 15(14). Labrum and mandibles clearly visible from above, the latter more or less opposable; antennae 10-segmented; antennal club cupuliform (Fig. 35.29A), the proximal segment circular and concave and the distal 2 segments fitting into it; hind tibiae without obliquely transverse ridges or groups of spines ..... **Hybosoridae** (p. 627)
- If labrum visible from above, antennal club not cupuliform, and hind tibiae with obliquely transverse ridges or groups of spines; if mandibles visible with opposable apices, antennae 9-segmented ..... **Scarabaeidae** (p. 627)
- 16(12). Segments of antennal club capable of close apposition; abdomen with 5 ventrites; mid coxal cavities contiguous (Fig. 35.15w); elytra dull and more or less tuberculate, without striae (Fig. 35.29G) ..... **Trogidae** (p. 627)
- Segments of antennal club not capable of close apposition; abdomen with 6 ventrites; mid coxal cavities distinctly separated; elytra shining and distinctly striate (Fig. 35.29F) ..... **Passalidae** (p. 627)
- 17(10). Elytra absent; wingless larviform females (Fig. 35.53B) ..... 18
- Elytra present (rarely reduced to small lobes) ..... 19
- 18(17). Median ocellus present; all tarsi 5-segmented; antennae very slender, 9-segmented ..... **Dermestidae** (*Thylocladus* females) (p. 642)
- Median ocellus absent; tarsi heteromorous (5-5-4) or all 4-segmented; antennae stouter, with 11 or fewer than 5 segments ..... **Rhipiphoridae-RHIPIDIINAE** (p. 663)
- 19(17). Minute somewhat flattened beetles, rarely more than 1 mm in length, with filamentous antennae, in which the segments (including those of the loose club) are elongate, narrow, and clothed with whorls of long hairs; hind wings almost always lined with fringe of long, fine hairs (Fig. 35.24A) (often visible at edge of elytra); hind wings absent in a few highly compact and eyeless forms; elytra usually more or less truncate exposing one or more tergites; hind coxae usually moderately to widely separated or hind coxae with well-developed plates; abdomen with 6 or 7 ventrites ..... **Ptilidae** (p. 619)
- Length usually more than 1 mm; antennae rarely filamentous; if wings fringed with long hairs, body more convex and abdomen with fewer than 6 ventrites ..... 20
- 20(19). Elytra usually completely covering abdominal tergites or exposing apex of one only; if 1 or 2 complete tergites exposed, then head without paired ocelli and first exposed tergite much shorter than elytra ..... 21
- Elytra almost always exposing 3 or more abdominal tergites (Figs 35.27A, B, 46F); if only 1 or 2 exposed, then head with paired ocelli or first exposed tergite longer than elytra ..... 242
- 21(20). Tarsus of mid leg with 5 distinct segments ..... 22
- Tarsus of mid leg pseudotetramerous (with 4 distinct segments plus a highly reduced penultimate segment, concealed by lobe of preceding segment) (Fig. 35.59F) ..... 158
- Tarsus of mid leg with 4 distinct segments ..... 192
- Tarsus of mid leg pseudotrimerous (with 3 distinct segments plus a highly reduced penultimate segment concealed within lobe of preceding segment) (Figs 35.49A-C) ..... 227
- Tarsus of mid leg with 3 distinct segments (or rarely fewer) ..... 229
- 22(21). Mid coxal cavities open laterally (partly closed by mesepimeron) (Figs 35.15T-V); pre-gular area never with laterally opening, setose cavities ..... 23
- Mid coxal cavities distinctly closed laterally by meeting of mesosternum and metasternum (Fig. 35.15W); or if open, pre-gular area with pair of laterally opening, setose cavities, transverse occipital ridge present (Fig. 35.15F), metasternum with paired femoral lines behind mid coxal cavities, body densely setose (Fig. 35.48F) ..... 125
- 23(22). Fore trochantins at least partly exposed (Figs 35.15J-M) ..... 24
- Fore trochantins completely concealed or apparently absent (Figs 35.15N-S) ..... 81
- 24(23). Antennae without a distinct club (sometimes gradually clavate (Fig. 35.15A)); antennal segment 8 not smaller than both 7 and 9; transverse occipital carina never combined with 6 ventrites ..... 25
- Antennae with distinct club consisting of from 1 to 7 segments (Figs 35.23E-G, 25B, 36C, 46B); if club weakly developed (Fig. 35.25C), then segment 8 smaller (either shorter or narrower or both) than segments 7 and 9 (in marginal cases, the head has a transverse occipital carina and there are 6 ventrites) ..... 53
- 25(24). Tarsal segments on hind leg at least as many as on mid leg ..... 26
- Tarsal segments on hind leg 1 less than on mid leg ..... 51
- 26(25). Antennal segments 9; antennae very slender, with last 3 segments greatly elongated; body yellowish brown ..... **Dermestidae** (*Thylocladus* males) (p. 642)
- Antennal segments 10; antennae in males often with basal segments enlarged and modified; soft-bodied, brightly coloured beetles (red or yellow on blue or black) (Fig. 35.45C) ..... **Melyridae-MALACHIINAE** (pt, p. 647)
- Antennal segments 11 (rarely more) ..... 27



27(26). Head without paired genal ridges beneath ..... 28  
Head with paired genal ridges beneath (Fig. 35.15G) which fit against edges of fore coxae (or occasionally the mid coxae); pronotum very short and broad ..... 50

28(27). Mesepisterna distinctly separated at midline, the distance between them more than 0.25 times mid coxal width (Figs 35.6B, 15U, W) ..... 29  
Mesepisterna meeting at midline, or separated by a distance less than 0.25 times mid coxal width (Figs 35.15T, V) ..... 49

29(28). Labrum free and mostly visible (Figs 35.15A–C) ..... 30  
Labrum entirely or almost entirely concealed beneath clypeus or solidly fused to clypeus (apparently absent) ..... 47

30(29). Body very short and broad, less than 1.5 times as long as wide ..... 31  
Body more than 1.5 times as long as wide ..... 33

31(30). Posterior edge of pronotum simple, not distinctly crenulate; antennal insertions concealed from above by projections of the frons (Fig. 35.15A); mid coxal cavities moderately to widely separated, by more than 0.4 times coxal width (Fig. 35.36B); apical segment of maxillary palp cylindrical to fusiform; body moderately to strongly convex ... 32  
Posterior edge of pronotum distinctly crenulate (Fig. 35.36D); antennal insertions exposed from above (Figs 35.15B–D); mid coxal cavities narrowly separated, by less than 0.4 times coxal width; apical segment of maxillary palp slightly to strongly expanded at apex; broad, flattened beetles clothed with decumbent hairs forming a pattern ..... **Psephenidae** (p. 635)

32(31). Metasternum without transverse suture; frontoclypeal suture absent; mid tarsi with at least one segment bearing a membranous appendage (Fig. 35.15Z); prosternum in front of coxae shorter than intercoxal process; body highly convex and often shiny and metallic in colour ..... **Byrrhidae** (pt, p. 634)  
Metasternum with transverse suture (Fig. 35.15U); frontoclypeal suture present (Fig. 35.15A); mid tarsi simple, the segments not lobed below, usually clothed with scattered setae only; prosternum in front of coxae longer than intercoxal process ..... **Limnichidae** (pt, p. 634)

33(30). Mid coxae separated by less than width of one coxa ..... 34  
Mid coxae separated by more than width of one coxa (Fig. 35.15U) ..... 44

34(33). Intercoxal process on ventrite 1 present ..... 35  
Intercoxal process on ventrite 1 absent ..... 40

35(34). Pronotum without produced and acute posterior angles (if posterior angles slightly produced, all coxae widely separated) ..... 36  
Pronotum with strongly produced and acute posterior angles (Fig. 35.15N); fore coxae and mid coxae narrowly separated and hind coxae contiguous; moderately broad and flattened beetles with pectinate or incrassate antennae. Known only from Windjana Gorge (near Derby, W.A.) ..... **Brachypsectridae** (p. 636)

36(35). Head prognathous or only slightly declined (Fig. 35.36C); all ventrites free or 1 and 2 connate; pronotum without paired basal pits or impressions ..... 37  
Head moderately to strongly hypognathous (Figs 35.36I, 46D); ventrites 1 to 3 connate; pronotum with paired basal pits or impressions ..... 38

37(36). Hind coxal plates well-developed and complete (Figs 35.36B, 42B); fore coxae externally transverse and not projecting below prosternum; intercoxal process of prosternum complete, extending behind coxae (Figs 35.15J, N); fore coxal cavities narrowly separated, by less than 0.4 times coxal width; mid tarsi with at least one segment bearing a membranous appendage (Fig. 35.15Z) ..... **Dascillidae** (p. 631)  
Hind coxal plates weakly developed to absent; fore coxae externally globular to conical and projecting well below prosternum (Fig. 35.15H); intercoxal process of prosternum incomplete, terminating between coxae (Figs 35.3C, 15K); fore coxal cavities contiguous or subcontiguous; mid tarsi simple, the segments not lobed below, usually clothed with scattered setae only ..... **Melyridae-DASYTINAE** (p. 647)

38(36). Body narrowly elongate, more than 3 times as long as wide; tarsi with empodium enlarged and multisetose (Fig. 35.15Y); large beetles (more than 10 mm long) with antennae flabellate in male (Fig. 35.37A) and pectinate in female (Fig. 35.37B) ..... **Callirhipidae** (p. 635)  
Body less than 3 times as long as wide; tarsi with empodium bisetose or absent ..... 39

39(38). Posterior edge of pronotum simple, not distinctly crenulate; antennae shorter than head and prothorax taken together; metasternum with transverse suture (Fig. 35.15U); transverse occipital ridge or carina absent; mid coxal cavities moderately to widely separated, by more than 0.4 times coxal width ..... **Elmidae-LARAINAE** (pt, p. 634)  
Posterior edge of pronotum distinctly crenulate (Fig. 35.15J); antennae much longer than head and prothorax taken together; metasternum without transverse suture; transverse occipital ridge or carina present (Fig. 35.15F); mid coxal cavities narrowly separated, by less than 0.4 times coxal width ..... **Ptilodactylidae-ANCHYTARSINAE** (p. 635)

40(34). Posterior edge of pronotum simple, not distinctly crenulate; tarsi with empodium bisetose or absent; fore coxal cavities contiguous or subcontiguous (Figs 35.15K, L); antennae, if flabellate, with 11 segments or fewer ..... 41  
Posterior edge of pronotum distinctly crenulate (Fig. 35.15J); tarsi with empodium enlarged and multisetose (Fig. 35.15Y); fore coxal cavities separated by prosternal process; antennae pectinate in female, flabellate in male and with more than 30 segments (Fig. 35.35) ..... **Rhipiceridae** (p. 631)

41(40). Antennal insertions moderately to widely separated, the distance between them at least 1.5 times and usually 2 times the diameter of one of them (Fig. 35.15B) ..... 42

- Antennal insertions approximate, the distance between them less than or only slightly greater than the diameter of one of them (Figs 35.15C, D) ..... 43
- 42(41). Frontoclypeal suture present; labrum membranous and usually partly concealed beneath clypeus (Fig. 35.15B); tarsal claws simple or toothed, but without membranous appendages; tarsal segment 4 strongly bilobed; pubescence more or less uniform, without scattered stiff, erect setae; without eversible membranous vesicles ..... **Cantharidae** (pt. p. 640)
- Frontoclypeal suture absent; labrum fully exposed and sclerotised; tarsal claws usually bearing membranous appendages; if tarsal segment 4 lobed, 3 lobed as well; vestiture with stiff, erect, dark setae scattered among the finer hairs; prothorax and base of abdomen often with eversible, membranous vesicles ..... **Melyridae-MALACHIINAE** (pt. p. 647)
- 43(41). Abdomen without luminous organ; eyes moderately large and well separated (Fig. 35.15C); hind trochanter with transverse or slightly oblique femoral attachment (Fig. 35.47L) ..... **Lycidae** (pt. p. 638)
- Abdomen with luminous organ (visible as yellowish white colour of last 2 ventrites) (Fig. 35.38D); eyes very large and approximate (Fig. 35.15D); hind trochanter with strongly oblique femoral attachment (Fig. 35.6B) ..... **Lampyridae** (pt. p. 640)
- 44(33). Mid tarsi simple, the segments not lobed below, usually clothed with scattered setae only (Fig. 35.15Y); all ventrites free or 1 to 3 connate; eyes entire ..... 45
- Mid tarsi with at least one segment lobed and usually densely setose below (Fig. 35.15AA); ventrites 1 to 5 connate; eyes partly divided by canthus ..... **Limnichidae** (*Paralimnichus*) (p. 634)
- Mid tarsi with at least one segment bearing a membranous appendage (Fig. 35.15Z); ventrites 1 and 2 connate, the suture between them usually incomplete or very weak; eyes entire; fore coxae globular; body often large and usually metallic or brightly coloured ..... **Buprestidae** (p. 632)
- 45(44). Body narrowly elongate, more than 3 times as long as wide, strongly flattened and glabrous; head abruptly constricted posteriorly to form a broad neck (Fig. 35.47C); hind coxal plates weakly developed to absent; mesosternum without cavity ..... **Cucujidae-CUCUJINAE** (pt. p. 651)
- Body less than 3 times as long as wide, neither strongly flattened nor glabrous; head not abruptly constricted posteriorly (sometimes gradually narrowed); hind coxal plates well-developed and complete (Figs 35.36B, 42B); mesosternum with distinct cavity into which apex of prosternal process is inserted (Fig. 35.15U) ..... 46
- 46(45). Antennae slender, segments 5 to 10 longer than wide; body ovoid, base of prothorax not narrower than combined elytral bases (Fig. 35.36A); pronotum without anterior constriction or basal carinae; hind coxae contiguous or very narrowly separated; ventrite 1 with 1 pair of curved femoral lines (Fig. 35.49D) .... **Limnichidae** (pt. p. 634)
- Antennae thicker, segments 5 to 10 transverse; body more elongate, base of prothorax narrower than combined elytral bases; pronotum constricted anteriorly or with paired longitudinal carinae at base; hind coxae moderately to widely separated; ventrite 1 without femoral lines ..... **Elmidae-LARAINAE** (pt. p. 634)
- 47(29). Body narrowly elongate, more than 3 times as long as wide; posterior edge of pronotum simple, not distinctly crenulate; intercoxal process on ventrite 1 acute (Fig. 35.47L) to narrowly rounded; antennal insertions exposed from above (Figs 35.15B, C); hind coxal plates weakly developed to absent ..... 48
- Body less than 3 times as long as wide; posterior edge of pronotum distinctly crenulate (Fig. 35.15J); intercoxal process on ventrite 1 broadly rounded to truncate (Fig. 35.48J); antennal insertions concealed from above by projections of the frons; hind coxal plates well-developed and complete (Fig. 35.36B); body ovoid (Fig. 35.36H); head strongly hypognathous, fitting into cavity at anterior edge of prosternum (Fig. 35.36I); legs strongly flattened and expanded, fitting into depressions on underside of body ..... **Chelonariidae** (p. 636)
- 48(47). Lateral pronotal carinae complete and sharply defined (Figs 35.46H, K, L); head prognathous or only slightly declined; fore coxae externally transverse and not projecting below prosternum (Fig. 35.15M); elytra impunctate or with confused punctation; clypeus transverse; body brown to black, shiny ..... **Cerambycidae** (*Parandra*) (p. 672)
- Lateral pronotal carinae absent; head moderately to strongly hypognathous (Fig. 35.36I); fore coxae externally conical and projecting well below prosternum (Fig. 35.15H); elytra with distinct puncture rows (Fig. 35.38H); clypeus longer than broad; body dull grey or brown ..... **Rhinorhipidae** (p. 636)
- 49(28). Intercoxal process on ventrite 1 absent; head abruptly constricted posteriorly to form a broad or narrow neck; antennae serrate (Fig. 35.38E) to pectinate (Fig. 35.37B); eyes shallowly emarginate or slightly covered by canthus (Fig. 35.15A); length greater than 7.5 mm ..... **Lymexylidae** (pt. p. 644)
- Intercoxal process on ventrite 1 present (Fig. 35.6B); head not abruptly constricted posteriorly (sometimes gradually narrowed); antennae filiform or incrassate (Fig. 35.45A); eyes entire; length less than 4 mm ..... **Melyridae-DASYTINAE** (p. 647)
- 50(27). Transverse occipital ridge or carina absent; mid tarsi with at least one segment lobed and usually densely setose below (Fig. 35.15AA); frontoclypeal suture absent or indistinct; without other characters in combination ..... **Scirtidae** (p. 624)
- Transverse occipital ridge or carina present (Fig. 35.15F); mid tarsi simple, the segments not lobed below, usually clothed with scattered setae only; frontoclypeal suture distinct (Fig. 35.15A); body more or less fusiform, more strongly tapered posteriorly; hind coxal plates large and oblique; mid and hind legs with fringes of dark spines at apices of tibiae and first 4 tarsal segments (Fig. 35.28A) ..... **Eucinidae** (p. 624)
- 51(25). Mesepisterna distinctly separated at midline, the distance between them more than 0.25 times mid coxal width (Fig.



- 35.6B); tarsal claws neither pectinate nor with bristle-like appendages; if head abruptly constricted posteriorly, neck broad and body strongly flattened ..... 52
- Mesepisterna meeting at midline, or separated by a distance less than 0.25 times mid coxal width (Fig. 35.15T); tarsal claws neither pectinate nor with bristle-like appendages; head not abruptly constricted posteriorly (sometimes gradually narrowed) (Figs 35.56B, C) ..... **Pythidae**-PILIPALPINAE (pt, p. 668)
- Mesepisterna broadly joined at midline, so that mesosternum is separated from anterior edge of mesothorax (Fig. 35.15V); tarsal claws pectinate and each with bristle-like appendage beneath; head abruptly constricted posteriorly to form narrow neck (Fig. 35.55C) ..... **Meloidae** (p. 668)
- 52(51). Mid coxae separated by less than width of one coxa (Fig. 35.15T); lateral pronotal carinae absent; head not abruptly constricted posteriorly (sometimes gradually narrowed) (Fig. 35.55B); fore coxae externally conical and projecting well below prosternum (Fig. 35.15H); body convex or slightly flattened, pubescent ..... **Oedemeridae** (p. 668)
- Mid coxae separated by more than width of one coxa (Fig. 35.15U); lateral pronotal carinae complete and sharply defined; head abruptly constricted posteriorly to form a broad neck (Fig. 35.47C); fore coxae externally globular and not projecting below prosternum (Fig. 35.15R); body strongly flattened and glabrous ..... **Cucujidae**-CUCUJINAE (pt, p. 651)
- 53(24). Antennal segments 7 to 9 ..... 54
- Antennal segments 10 ..... 56
- Antennal segments 11 ..... 59
- 54(53). First antennal segment always short and broad, irregularly shaped, never elongate; antennal segments each with several to many conspicuous setae; antennal club not preceded by cupule; maxillary palp rarely more than half as long as antenna; body oval to slightly elongate and strongly flattened .... **Trogossitidae**-LOPHOCATERINAE (p. 645)
- First antennal segment always much longer than broad; antennal segments preceding club glabrous, that immediately preceding club almost always forming transverse, cup-like segment (cupule) (Figs 35.23E-G); maxillary palp much more than half as long as antenna; body usually moderately to strongly convex ..... 55
- 55(54). Antennal club 3-segmented; number of abdominal ventrites almost always 5 (if 6, then body oval and convex and elytra completely concealing abdominal apex) ..... **Hydrophilidae** (pt, p. 617)
- Antennal club 5- or 6-segmented; number of abdominal ventrites 6 or 7; if body oval and convex, then elytra truncate, exposing abdominal apex ..... **Hydraenidae** (pt, p. 619)
- 56(53). Ventrites 5; antennal insertions exposed from above (Figs 35.15B-E); antennal club with 3 or fewer segments ..... 57
- Ventrites 6; antennal insertions concealed from above by projections of the frons (Fig. 35.15A); antennal club 4-segmented ..... **Leiodidae** (*Zeadolopus*) (p. 619)
- 57(56). Mandibles without dorsal tubercles; frontoclypeal suture absent or indistinct; metasternal longitudinal suture absent ..... 58
- Mandibles each with dorsal tubercle; frontoclypeal suture distinct and strongly curved (Fig. 35.15E); metasternal longitudinal suture moderately to very long (more than 0.25 times as long as body of sternite) ..... **Sphindidae** (pt, p. 649)
- 58(57). Head prognathous or only slightly declined (Fig. 35.46L); transverse occipital ridge or carina absent; intercoxal process of prosternum complete, extending behind coxae (Figs 35.15J, M); outer edge of mid tibia bearing spines or teeth along most of its length; body ovate to elongate and strongly flattened ..... **Trogossitidae**-LOPHOCATERINAE (pt, p. 645)
- Head moderately to strongly hypognathous (Fig. 35.46D); transverse occipital ridge or carina present (Fig. 35.15F); intercoxal process of prosternum incomplete, terminating between coxae (Fig. 35.3C); outer edge of mid tibia simple; minute, globular beetles clothed with decumbent hairs which form whorls (Fig. 35.44E) ..... **Trogossitidae**-RENTONIINAE (pt, p. 645)
- 59(53). Ventrites 4 or 5 ..... 60
- Ventrites 6 ..... 78
- Ventrites 7; large, flattened, yellowish brown beetles with raised tubercles on elytra (Fig. 35.25F) ..... **Silphidae** (*Ptomaphila*) (p. 621)
- 60(59). Head prognathous or only slightly declined (Figs 35.46E-L) ..... 61
- Head moderately to strongly hypognathous (Fig. 35.46D) ..... 76
- 61(60). Antennal club not 5-segmented or with 2nd segment subequal to or larger than 1st ..... 62
- Antennal club 5-segmented with 2nd segment smaller (shorter or narrower or both) than 1st (Figs 35.25C, D) ..... 75
- 62(61). Intercoxal process on ventrite 1 acute (Fig. 35.47L) to narrowly rounded ..... 63
- Intercoxal process on ventrite 1 broadly rounded to truncate (Fig. 35.48J) ..... 72
- 63(62). Lateral pronotal carinae complete and sharply defined (Figs 35.46J-L); all ventrites free or 1 and 2 connate ..... 64
- Lateral pronotal carinae absent (Fig. 35.46I); ventrites 1 to 3 connate; surfaces of pronotum and elytra tuberculate and shiny, with scattered, erect hairs ..... **Phloeostichidae** (*Hymaea*) (p. 650)
- 64(63). Fore coxal cavities externally open (Figs 35.15J-O) ..... 65
- Fore coxal cavities externally closed (Figs 35.15P-R) ..... 70
- 65(64). Antennal club 4- or 5-segmented; fore tarsi often strongly expanded and setose; body oblong, convex and densely clothed with decumbent hairs; frontoclypeal suture absent ..... **Leiodidae** (*Colan*) (pt, p. 619)
- Antennal club with 3 segments or fewer; fore tarsi not strongly expanded and setose; if frontoclypeal suture absent, body more elongate, flattened or glabrous ..... 66

- 66(65). Fore coxal cavities contiguous or subcontiguous; pronotal hypomera each with large, flat-bottomed pit (Fig. 35.15K); vestiture including scattered, erect, stiff setae ..... **Acanthocnemidae** (p. 646)  
Fore coxal cavities distinctly separated by prosternal process (Figs 35.15J, M, Q); without hypomeral pits or scattered stiff setae ..... 67
- 67(66). Body more or less flattened with pronotum laterally explanate (Figs 35.46J–L); fore coxae strongly transverse with widely exposed trochantins; hind coxae extending laterally to meet elytral epipleura, so that metapleura are separated from front angles of ventrite 1 ..... **Trogossitidae**-LOPHOCATERINAE (pt, p. 645)  
If body flattened, pronotum not laterally explanate; fore coxae less strongly transverse and trochantins only partly exposed (sometimes only barely visible within slit-like extension of coxal cavity); hind coxae separated from elytral epipleura by extensions of the metapleura, which meet the front angles of ventrite 1 ..... 68
- 68(67). Frontoclypeal suture distinct; mandibles with dorsal tubercle which fits into lateral cavity on clypeus (Fig. 35.15E); body oblong, moderately convex and pubescent ..... **Hobartiidae** (pt, p. 653)  
Frontoclypeal suture absent; mandibles without dorsal tubercle; body flattened and parallel-sided or glabrous ..... 69
- 69(68). Body flattened and parallel-sided, pubescent; transverse occipital carina present (Fig. 35.15F); lateral pronotal carinae finely crenulate or denticulate (Fig. 35.46L); first ventrite about 2 times as long as 2nd, with pair of setose impressions in male ..... **Phloeostichidae** (*Myrabolia*) (pt, p. 650)  
Body moderately convex and glabrous; transverse occipital carina absent; lateral pronotal carinae simple (Fig. 35.48A); first ventrite only slightly longer than 2nd, without paired impressions ..... **Lamingtoniidae** (p. 653)
- 70(64). Lateral pronotal carinae simple; without other characters in combination ..... 71  
Lateral pronotal carinae crenulate; body elongate and somewhat flattened; elytra with rows of deep punctures and short, weak, irregularly placed, longitudinal ridges (Fig. 35.46A); epipleura moderately broad and complete ..... **Protocucujidae** (p. 649)
- 71(70). Antennal club ovate, as long as or slightly longer than wide, symmetrical; body ovate or oblong; prothorax not constricted posteriorly, its base as wide as or slightly narrower than combined elytral bases; body shape variable but vestiture never of flattened scales ..... **Nitidulidae** (pt, p. 649)  
Antennal club at least 2 times as long as wide, asymmetrical; body almost always elongate and parallel-sided; prothorax constricted posteriorly, so that its base is distinctly narrower than combined elytral bases; body flattened and either glabrous or clothed with flattened scales (Fig. 35.44D) ..... **Trogossitidae**-TROGOSSITINAE (pt, p. 645)
- 72(62). Hind coxal plates well-developed and complete (Fig. 35.42B); antennal insertions concealed from above by projections of the frons (Fig. 35.42A) ..... **Nosodendridae** (p. 642)  
Hind coxal plates weakly developed to absent; antennal insertions exposed from above (Figs 35.46J, K) ..... 73
- 73(72). Mid coxae separated by less than width of one coxa; lateral pronotal carinae simple; fore coxal cavities internally closed (Fig. 35.15O); without other characters in combination ..... 74  
Mid coxae separated by more than width of one coxa (Fig. 35.15U); lateral pronotal carinae broadly crenulate (Fig. 35.46J); fore coxal cavities internally open (Fig. 35.15M); body broad and somewhat flattened; pronotum laterally explanate; elytra bearing tubercles covered with stiff, curled hairs, which are often concealed beneath debris ..... **Phloeostichidae** (*Priastichus*) (p. 650)
- 74(73). Pronotum without paired setose cavities; elytral apices without distinct apical gap when in place ..... **Nitidulidae** (pt, p. 649)  
Pronotum with large, setose cavities at posterior angles (Fig. 35.46K); elytral apices with distinct apical gap when in place (caused by deflection of sutural flange) ..... **Phloeostichidae** (*Tasmosalpingus*) (p. 650)
- 75(61). Mandibles without dorsal tubercles; fore coxae externally globular to conical and projecting well below prosternum (Fig. 35.3C); intercoxal process of prosternum incomplete, terminating between coxae; mid coxal cavities contiguous or subcontiguous (Fig. 35.15W) ..... **Leiodidae** (pt, p. 619)  
Mandibles each with dorsal tubercle which fits into lateral cavity in clypeus (Fig. 35.15E); fore coxae externally transverse and not projecting below prosternum (Fig. 35.15M); intercoxal process of prosternum complete, extending behind coxae; mid coxal cavities moderately to widely separated, by more than 0.4 times coxal width ..... **Hobartiidae** (pt, p. 653)
- 76(60). Antennal insertions located laterally under a slight ridge and not easily visible from above; body very short and broad, less than 1.5 times as long as wide, and strongly convex; mesosternum with distinct cavity into which apex of prosternal process is inserted (Fig. 35.15U) ..... **Byrrhidae** (pt, p. 634)  
Antennal insertions located dorsally between the eyes and easily visible from above; if body very short, broad and strongly convex, mesosternal cavity absent ..... 77
- 77(76). Body minute (less than 1.5 mm long) and globose; hind coxae flat, not excavate, without coxal plates; ventrite 1 longer than following 2 taken together; head without median ocellus ..... **Trogossitidae**-RENTONIINAE (pt, p. 645)  
Body larger (usually more than 1.5 mm long), more elongate and/or flattened; hind coxae excavate, with coxal plates which conceal at least bases of femora; ventrite 1 not as long as following 2 taken together; head usually with median ocellus ..... **Dermestidae** (pt, p. 642)
- 78(59). Antennal club not 5-segmented or with 2nd segment subequal to or larger than 1st ..... 79  
Antennal club 5-segmented, 2nd segment smaller (shorter or narrower or both) than 1st ..... **Leiodidae** (pt, p. 619)
- 79(78). Fore coxal cavities externally open; fore coxae globular to conical and projecting well below prosternal process, which is incomplete, terminating between coxae (Fig. 35.3C) ..... 80  
Fore coxal cavities externally closed; fore coxae externally transverse and not projecting below prosternal process,



- which is complete, extending behind coxae (Fig. 35.15M) ..... **Nitidulidae** (pt, p. 649)
- 80(79). Antennal club 3-segmented; elytra truncate at apex, exposing abdominal apex; paired ocelli sometimes visible between eyes; hind coxal plates well-developed but incomplete ..... **Staphylinidae** (*Microsilpha*) (p. 621)
- Antennal club 4- or 5-segmented; elytra not truncate, concealing abdominal apex; paired ocelli absent; hind coxal plates weakly developed to absent ..... **Leiodidae** (*Colon*) (pt, p. 619)
- 81(23). Antennal segments 11 (or rarely more) ..... 82
- Antennal segments fewer than 11 ..... 118
- 82(81). Tarsal segments on hind leg at least as many as on mid leg ..... 83
- Tarsal segments on hind leg 1 less than on mid leg ..... 97
- 83(82). Pronotum without produced and acute posterior angles ..... 84
- Pronotum with strongly produced and acute posterior angles (Fig. 35.15N) ..... 94
- 84(83). Ventrites 5 ..... 85
- Ventrites 6 ..... **Cleridae** (pt, p. 645)
- 85(84). Intercoxal process of prosternum not or only slightly, gradually expanded at apex (Figs 35.15J, M, Q) ..... 86
- Intercoxal process of prosternum strongly and usually abruptly expanded at apex (Figs 35.15P, 48J) ..... 92
- 86(85). Fore coxal cavities externally open (Figs 35.3C, 15M, O) ..... 87
- Fore coxal cavities externally closed (Fig. 35.15R) ..... **Silvanidae-SILVANINAE** (p. 651)
- 87(86). Antennae without a distinct club (sometimes gradually clavate) (Fig. 35.15A) ..... 88
- Antennae with a distinct club consisting of from 1 to 7 segments (Figs 35.42G, 47I-K) ..... 90
- 88(87). Body narrowly elongate, more than 3 times as long as wide; head abruptly constricted posteriorly to form a broad neck (Figs 35.47B, C); antennal scape more than 3 times as long as pedicel; head prognathous or only slightly declined ..... **Silvanidae-ULEIOTINAE** (p. 651)
- Body less than 3 times as long as wide; head not abruptly constricted posteriorly (sometimes gradually narrowed); antennal scape less than 3 times as long as pedicel; head moderately to strongly hypognathous (Figs 35.42D, G) ..... 89
- 89(88). Mid coxae separated by less than width of one coxa; metasternum without transverse suture; hind coxal plates well-developed and complete (Fig. 35.42B); head with a single median ocellus (Fig. 35.42D) ..... **Dermestidae** (pt, p. 642)
- Mid coxae separated by more than width of one coxa; metasternum with transverse suture (Fig. 35.15U); hind coxal plates weakly developed to absent ..... **Elmidae-ELMINAE** (p. 634)
- 90(87). Mid coxae separated by less than width of one coxa; antenna not geniculate, scape less than 3 times as long as pedicel; elytra concealing abdominal tergites or exposing apex of one only ..... 91
- Mid coxae separated by more than width of one coxa; antenna geniculate, scape more than 3 times as long as pedicel; elytra truncate, exposing at least one abdominal tergite (Fig. 35.23K) ..... **Histeridae** (pt, p. 618)
- 91(90). Hind coxal plates well-developed and complete (Fig. 35.42B); head with a single median ocellus (Fig. 35.42D); head moderately to strongly hypognathous; frons simple ..... **Dermestidae** (pt, p. 642)
- Hind coxal plates weakly developed to absent; head without ocelli; head prognathous or only slightly declined; frons with a pair of small cavities usually joined by a strongly arched groove (Fig. 35.47J) ..... **Cavognathidae** (p. 653)
- 92(85). Mid coxae separated by less than width of one coxa; intercoxal process on ventrite 1 acute (Fig. 35.47L) to narrowly rounded; pronotum without lateral, submarginal lines or ridges; lateral pronotal carinae crenulate (Fig. 35.46L) or dentate (Fig. 35.40) ..... 93
- Mid coxae separated by more than width of one coxa; intercoxal process on ventrite 1 broadly rounded to truncate (Fig. 35.48J); pronotum with lateral, submarginal lines or ridges (Fig. 35.47E); lateral pronotal carinae usually simple ..... **Laemophloeidae** (pt, p. 651)
- 93(92). Fore coxal cavities externally open (Figs 35.15M, O); hind coxae moderately to widely separated, without coxal plates (Fig. 35.48J); ventrite 1 without femoral lines; ocelli absent ..... **Phloeostichidae** (*Myrabolia*) (pt, p. 650)
- Fore coxal cavities externally closed (Figs 35.15P, Q); hind coxae contiguous or narrowly separated, with well-developed and complete coxal plates (Figs 35.36B, 42B); ventrite 1 with 1 pair of straight femoral lines; head with paired ocelli (Fig. 35.40) ..... **Derodontidae** (p. 641)
- 94(83). Labrum free and mostly visible ..... 95
- Labrum entirely or almost entirely concealed beneath clypeus or solidly fused to clypeus (apparently absent) ..... **Eucnemidae** (p. 637)
- 95(94). Hind coxae contiguous or narrowly separated and intercoxal process on ventrite 1 acute or narrowly rounded (Fig. 35.47L) ..... 96
- Hind coxae moderately to very widely separated and intercoxal process on ventrite 1 broadly rounded or truncate (Fig. 35.48J) ..... **Elateridae** (*Anischia*) (p. 637)
- 96(95). Ventrites 1 to 4 connate; antennae never clubbed; body usually elongate and parallel-sided; metasternum and abdomen without tarsal grooves ..... **Elateridae** (pt, p. 637)
- Ventrites 1 to 5 connate; antennae almost always with 3-segmented club; body almost always somewhat flattened and tapering anteriorly and posteriorly from junction of pronotum and elytra; if antennae not clubbed and body parallel-sided, then metasternum and abdomen with tarsal grooves ..... **Throscidae** (p. 637)
- 97(82). Mid coxae separated by less than width of one coxa ..... 98

- Mid coxae separated by more than width of one coxa ..... 114
- 98(97). Fore coxal cavities externally open (Fig. 35.15o) ..... 99
- Fore coxal cavities externally closed (Figs 35.15Q, R) ..... 109
- 99(98). Antennae without a distinct club (sometimes gradually clavate) ..... 100
- Antennae with a distinct club consisting of 3 segments (Figs 35.46L, 57F) ..... 108
- 100(99). Mid tarsi without lobed segments ..... 101
- Mid tarsi with lobed segments including the penultimate (Fig. 35.15AA) ..... 104
- Mid tarsi with lobed segments not including the penultimate (Fig. 35.59F); abdomen usually with only 4 ventrites, or if 5 are present, then the suture between the first 2 is weak or incomplete; length rarely exceeding 3.5 mm ..... **Aderidae** (pt, p. 671)
- 101(100). Lateral pronotal carinae complete and sharply defined (Fig. 35.54G) ..... 102
- Lateral pronotal carinae incomplete anteriorly (Fig. 35.53D) to absent (Figs 35.54H, I, 56A–C) ..... 103
- 102(101). Body narrowly elongate, more than 3 times as long as wide and glabrous; antennal scape less than 3 times as long as pedicel; fore coxae externally globular (Fig. 35.15Q). Known only from Tas. .... **Tenebrionidae** (*Tanylypa*) (p. 665)
- Body less than 3 times as long as wide and pubescent; antennal scape more than 3 times as long as pedicel; fore coxae externally transverse (Fig. 35.15M). Occurring in Papua New Guinea, not yet known from Australia ..... **Pterogeniidae**
- 103(101). Head prognathous or only slightly declined (Fig. 35.56A); fore coxal cavities internally open (Fig. 35.3C); body not laterally compressed; head not abruptly constricted posteriorly; tarsal claws simple ..... **Pythidae-PYTHINAE** (p. 668)
- Head moderately to strongly hypognathous (Fig. 35.53D); fore coxal cavities internally closed (Fig. 35.15O); body laterally compressed and wedge-shaped (Fig. 35.53D) or head abruptly constricted posteriorly to form narrow neck; tarsal claws pectinate or deeply bifid ..... **Rhipiphoridae** (pt, p. 663)
- 104(100). Head not abruptly constricted posteriorly (sometimes gradually narrowed) (Fig. 35.56B) ..... 105
- Head abruptly constricted posteriorly to form narrow neck (Figs 35.57G, H) ..... 107
- 105(104). Head moderately to strongly hypognathous (Fig. 35.51C); eyes shallowly emarginate; base of prothorax not or only slightly narrower than combined elytral bases; tibial spurs serrate ..... **Melandryidae** (pt, p. 662)
- Head prognathous or only slightly declined (Fig. 35.57F); eyes entire; base of prothorax distinctly narrower than combined elytral bases (Figs 35.56B, 57F); tibial spurs simple ..... 106
- 106(105). Antennal insertions concealed from above by projections of frons (Fig. 35.15A); pronotum distinctly longer than wide; ventrites 1 and 2 connate ..... **Anthicidae** (*Lagrioida*) (pt, p. 671)
- Antennal insertions exposed from above (Fig. 35.15B); pronotum not as long as broad; all ventrites free ..... **Pythidae-PILIPALPINAE** (pt, p. 668)
- 107(104). Eyes strongly emarginate (Fig. 35.57I); tibial spurs pubescent; intercoxal process on ventrite 1 absent ..... **Scaptiidae** (p. 671)
- Eyes not or only slightly emarginate; tibial spurs simple; intercoxal process on ventrite 1 acute to broadly rounded ..... **Anthicidae** (pt, p. 671)
- 108(99). Lateral pronotal carinae absent (Fig. 35.57F); base of prothorax distinctly narrower than combined elytral bases; intercoxal process of prosternum incomplete and acute at apex (Fig. 35.15O); mesepisterna meeting at midline, or separated by a distance less than 0.25 times mid coxal width (Fig. 35.15T); body not flattened ..... **Anthicidae** (*Lagrioida*) (pt, p. 671)
- Lateral pronotal carinae complete and sharply defined (Fig. 35.46L); base of prothorax as wide as or slightly narrower than combined elytral bases; intercoxal process of prosternum complete, strongly and usually abruptly expanded at apex (Figs 35.15P, 48I); mesepisterna distinctly separated at midline, the distance between them more than 0.25 times mid coxal width (Fig. 35.6B); body strongly flattened ..... **Phloeostichidae** (*Myrabolia*) (pt, p. 650)
- 109(98). Intercoxal process of prosternum not or only slightly, gradually expanded at apex (Figs 35.15J, M, Q) ..... 110
- Intercoxal process of prosternum strongly and usually abruptly expanded at apex (Figs 35.15P, 48J) ..... 111
- 110(109). Antennal insertions exposed from above (Fig. 35.15B); intercoxal process of prosternum incomplete, terminating between coxae (Fig. 35.15O); all ventrites free or 1 and 2 connate ..... **Anthicidae** (pt, p. 671)
- Antennal insertions concealed from above by projections of the frons (Fig. 35.15A); intercoxal process of prosternum complete, extending behind coxae (Fig. 35.15Q); ventrites 1 to 3 connate ..... **Tenebrionidae** (pt, p. 665)
- 111(109). Body narrowly elongate, more than 3 times as long as wide; mesepisterna meeting at midline, or separated by a distance less than 0.25 times mid coxal width (Fig. 35.15T); apical segment of labial palp slightly to strongly expanded at apex ..... **Chalcodryidae** (*Sirrhias*) (p. 665)
- Body less than 3 times as long as wide; mesepisterna distinctly separated at midline, the distance between them more than 0.25 times mid coxal width (Fig. 35.6B); apical segment of labial palp cylindrical to fusiform ..... 112
- 112(111). Lateral pronotal carinae complete and sharply defined (Fig. 35.51A); metasternum distinctly longer than first ventrite; body densely clothed with setae and/or scales ..... 113
- Lateral pronotal carinae absent; metasternum subequal to or shorter than first ventrite; body glabrous ..... **Zopheridae** (*Melytra*) (p. 664)
- 113(112). Antennal insertions exposed from above (Fig. 35.15B); frontoclypeal suture absent or indistinct; ventrites 1 to 3 con-



nate; fore coxal cavities internally open (Fig. 35.15P); body more elongate and vestiture consisting of coarser setae or scales ..... **Zopheridae-ULODINAE** (p. 664)

Antennal insertions concealed from above by projections of the frons (Fig. 35.15A); frontoclypeal suture distinct; ventrites 1 and 2 connate; fore coxal cavities internally closed (Fig. 35.15Q); body ovoid and vestiture consisting of fine, recumbent hairs ..... **Archeocrypticidae** (pt, p. 660)

114(97). Intercoxal process of prosternum not or only slightly, gradually expanded at apex (Figs 35.15J, M, Q) ..... 115  
Intercoxal process of prosternum strongly and usually abruptly expanded at apex (Figs 35.15P, 48J) ..... 117

115(114). Fore coxal cavities externally open (Figs 35.3C, 15M, O); all ventrites free or 1 and 2 connate; elytra exposing most of one abdominal tergite; body either short and broad, less than 2 times as long as wide, or laterally compressed and wedge-like ..... 116

Fore coxal cavities externally closed (Fig. 35.15Q); ventrites 1 to 3 connate; elytra concealing abdominal tergites or exposing apex of one only; body elongate, more than 2 times as long as wide, and strongly flattened ..... **Tenebrionidae** (*Platycotylus*) (p. 665)

116(115). Antennae without a distinct club (sometimes gradually clavate) (Fig. 35.15A); abdominal apex produced beyond elytral apices to form spine (Fig. 35.51D); hind coxae large, flattened, contiguous and fused to metasternum; head abruptly constricted posteriorly to form narrow neck, but closely appressed to prothorax so that neck is concealed; body laterally compressed and more or less wedge-shaped, pubescent ..... **Mordellidae** (p. 663)

Antennae with a distinct club consisting of 1 or 3 segments; abdominal apex not forming spine; hind coxae smaller, freely movable and widely separated; head not abruptly constricted posteriorly; body not laterally compressed or wedge-like, glabrous ..... **Histeridae-Acridini** (p. 618)

117(114). Hind coxae contiguous or narrowly separated and intercoxal process on ventrite 1 acute or narrowly rounded (Fig. 35.47L); antennal insertions concealed from above by projections of the frons (Fig. 35.15A); prosternum in front of coxae shorter than intercoxal process; fore coxal cavities internally closed (Fig. 35.15Q); body more ovoid and moderately convex ..... **Archeocrypticidae** (pt, p. 660)

Hind coxae moderately to very widely separated and intercoxal process on ventrite 1 broadly rounded or truncate (Fig. 35.48J); antennal insertions exposed from above (Fig. 35.15B); prosternum in front of coxae longer than intercoxal process; fore coxal cavities internally open (Fig. 35.15M); body more elongate, parallel-sided and usually flattened ..... **Laemophloeidae** (pt, p. 651)

118(81). Fore coxal cavities externally open (Figs 35.3C, 15M, O) ..... 119  
Fore coxal cavities externally closed (Figs 35.15P-R) ..... 123

119(118). Mid coxae separated by less than width of one coxa; hind coxae contiguous or narrowly separated and intercoxal process on ventrite 1 acute or narrowly rounded (Figs 35.6B, 47L); antenna 9-segmented, with a 3-segmented club, which is preceded by a strongly transverse, glabrous, cup-like segment (cupule) (Figs 35.23E-G); tibiae usually spiny; maxillary palps usually longer than antennae (Figs 35.23D, I) ..... **Hydrophilidae** (pt, p. 617)

Mid coxae separated by more than width of one coxa (Fig. 35.15U); hind coxae moderately to very widely separated and intercoxal process on ventrite 1 broadly rounded or truncate (Fig. 35.48J) ..... 120

120(119). Elytra truncate, exposing at least 1 abdominal tergite; antennae geniculate with scape more than 3 times as long as pedicel; upper surfaces usually smooth, shiny and glabrous (Fig. 35.23K) ..... **Histeridae** (pt, p. 618)

Elytra concealing abdominal tergites or exposing apex of one only; antennae not geniculate; scape less than 3 times as long as pedicel; upper surfaces tuberculate and dull or setose ..... 121

121(120). Antennal club 6-segmented and pectinate; prosternum in front of coxae very long, extending beneath head as chin piece (Fig. 35.15N); last tarsal segment longer than first 4 combined. Occurring in New Guinea; not yet known in Australia ..... **Dryopidae**

Antennal club with 3 segments or fewer; prosternum relatively short, not forming chin piece; last tarsal segment much shorter than first 4 combined ..... 122

122(121). Head moderately to strongly hypognathous; antenna 7- or 9-segmented with compact club, which may be undivided or indistinctly divided into 3 parts; upper surfaces tuberculate; elytra costate (Figs 35.23B, C) ..... **Hydrophilidae** (*Georissus*) (pt, p. 617)

Head prognathous or only slightly declined; antenna 10-segmented with distinctly 3-segmented, elongate club; upper surfaces smooth and densely setose; elytra not costate ..... **Sphindidae** (pt, p. 649)

123(118). Antennae with 10 segments; head without elongate rostrum; pronotum without lateral submarginal lines, ridges or carinae ..... 124

Antennae with 8 or 9 segments; head with rostrum which is longer than it is broad (Figs 35.57C, 61A, C); pronotum with lateral, submarginal lines, ridges or carinae ..... **Silvanidae** (*Nepharis*, *Nepharinus*) (p. 651)

124(123). Ventrites 5; fore coxae externally globular and not projecting below prosternum (Fig. 35.48J); antennal club 2-segmented or 1-segmented and globular (Fig. 35.46G) ..... **Rhizophagidae** (pt, p. 650)

Ventrites 6; fore coxae externally conical and projecting well below prosternum (Figs 35.15H, S); antennal club 1-segmented and much longer than wide ..... **Cleridae** (*Monophylla*) (p. 645)

125(22). Tarsal segments on hind leg at least as many as on mid leg ..... 126  
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126(125). Fore coxal cavities externally open (Figs 35.3C, 15J-O) ..... 127  
Fore coxal cavities externally closed (Figs 35.15P-S) ..... 138

127(126). Ventrites 5 ..... 128

- Ventrites 6 ..... 137
- 128(127). Antennae without a distinct club (sometimes gradually clavate) (Fig. 35.15A) ..... 129
- Antennae with a distinct club consisting of from 1 to 7 segments (Figs 35.42H, I, 47I-K) ..... 132
- 129(128). Pronotum without produced and acute posterior angles; antennal insertions exposed from above (Fig. 35.15B) ..... 130
- Pronotum with strongly produced and acute posterior angles (Fig. 35.15N); antennal insertions concealed from above by projections of the frons (Fig. 35.15A) ..... **Elateridae** (pt, p. 637)
- 130(129). Body elongate, parallel-sided and glabrous (Fig. 35.47D); length almost always more than 10 mm; head prognathous; prosternum in front of coxae well-developed, much longer than length of coxal cavity ..... **Cucujidae-PASSANDRINAE** (p. 651)
- Body usually shorter and broader, or if elongate, then not glabrous; length less than 8 mm; head strongly deflexed; prosternum reduced and shorter than length of coxal cavity ..... 131
- 131(130). Ventrites 1 and 2 connate; antennal insertions well separated; hind coxae contiguous and excavate to receive femora (with coxal plates) ..... **Anobiidae** (pt, p. 643)
- Ventrites 1 to 3 connate; antennal insertions almost always approximate (separated by less than length of scape); hind coxae widely separated and not excavate (without coxal plates) ..... **Anobiidae-PTININAE** (pt, p. 643)
- 132(128). Head prognathous or only slightly declined (Fig. 35.47F) ..... 133
- Head moderately to strongly hypognathous (Figs 35.42H, I) ..... 135
- 133(132). Body very short and broad, less than 1.5 times as long as wide; pronotum with median endocarina (visible as distinct line) (Fig. 35.47F); pronotum with lateral submarginal lines, ridges or carinae ..... **Propalticidae** (p. 651)
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- 134(133). Elytral epipleura absent or incomplete; ventrite 1 much longer than 2 (Fig. 35.47L); elytral apices with distinct apical gap when in place (caused by deflection of sutural flange) ..... **Cryptophagidae** (pt, p. 653)
- Elytral epipleura complete, extending to apex (Fig. 35.48J); ventrite 1 not or only slightly longer than 2; elytral apices without distinct apical gap when in place ..... **Languriidae-XENOSCELINAE** (pt, p. 654)
- 135(132). Outer edge of mid tibia simple; frontoclypeal suture absent or indistinct; hind trochanter with transverse or slightly oblique femoral attachment (Fig. 35.47L) ..... 136
- Outer edge of mid tibia bearing spines or teeth along most of its length (Figs 35.36B, C); frontoclypeal suture distinct (Figs 35.36B, C); hind trochanter with strongly oblique femoral attachment (Fig. 35.6B) ..... **Bostrichidae** (pt, p. 642)
- 136(135). All ventrites free or 1 and 2 connate ..... **Anobiidae** (pt, p. 643)
- Ventrites 1 to 3 connate ..... **Anobiidae-PTININAE** (pt, p. 643)
- 137(127). Mid coxal cavities narrowly separated, by less than 0.4 times coxal width; metasternal longitudinal suture absent; elytra usually concealing most of abdominal apex or exposing only part of one tergite; body pubescent, usually constricted at junction of prothorax and elytra, producing an ant-like appearance (if not, then prothorax with paired basal impressions) ..... **Scydmaenidae** (p. 621)
- Mid coxal cavities moderately to widely separated, by more than 0.4 times coxal width (Fig. 35.15U); metasternal longitudinal suture moderately to very long (more than 0.25 times as long as body of sternite) (Fig. 35.6B); elytra truncate, exposing at least one complete tergite (Fig. 35.25G); body subglabrous, without constriction between prothorax and elytra; pronotum simple, without basal impressions ..... **Staphylinidae-SCAPHIDIINAE** (p. 621)
- 138(126). Fore trochantins at least partly exposed (Figs 35.3C, 15M) ..... **Trogossitidae-EGOLIINAE** (p. 645)
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- 139(138). Antennal segments 11 (or rarely more) ..... 140
- Antennal segments fewer than 11 ..... 145
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- 141(140). Intercoxal process of prosternum not or only slightly, gradually expanded at apex (Fig. 35.15Q); pre-gular area with pair of laterally-opening, setose cavities; mid coxal cavities open laterally (partly closed by epimeron) (Figs 35.15T-V); metasternum with paired femoral lines behind mid coxal cavities; pronotum with lateral submarginal lines, ridges or carinae (Fig. 35.48F) ..... **Biphyllidae** (pt, p. 654)
- Intercoxal process of prosternum strongly and usually abruptly expanded at apex (Figs 35.15P, 48J); pre-gular area without laterally-opening, setose cavities; mid coxal cavities distinctly closed laterally by meeting of mesosternum and metasternum (Fig. 35.15W); metasternum without femoral lines behind mid coxal cavities; pronotum without lateral submarginal lines, ridges or carinae ..... 142
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- Labrum entirely or almost entirely concealed beneath clypeus or solidly fused to clypeus (apparently absent); antennal scape more than 3 times as long as pedicel; antennae geniculate (Fig. 35.62J); outer edge of mid tibia bearing spines or teeth along most of its length (Fig. 35.62O) ..... **Curculionidae-SCOLYTINAE** (pt, p. 682)
- 144(143). Antennal club 2-segmented; hind coxae moderately to very widely separated and intercoxal process on ventrite 1 broadly rounded or truncate (Fig. 35.48J); fore coxae externally globular and not projecting below prosternum



	(Figs 35.15Q, R); mid coxal cavities moderately to widely separated, by more than 0.4 times coxal width (Fig. 35.15U) .....	<b>Bostrichidae-LYCTINAE</b> (p. 642)
	Antennal club 3-segmented; hind coxae contiguous or narrowly separated and intercoxal process on ventrite 1 acute or narrowly rounded (Fig. 35.6B); fore coxae externally globular to conical and projecting well below prosternum (Figs 35.15H, S); mid coxal cavities narrowly separated, by less than 0.4 times coxal width .....	<b>Cleridae</b> (pt, p. 645)
145(139).	Labrum free and mostly visible (Figs 35.15A–D); lateral pronotal carinae complete and sharply defined (Fig. 35.23D); head abruptly constricted posteriorly to form a broad or narrow neck; antennal scape less than 3 times as long as pedicel; antenna with a 3-segmented, loose, symmetrical club, which is finely, densely and uniformly pubescent, and preceded by a strongly transverse, glabrous cup-like segment (cupule) (Fig. 35.23G) .....	<b>Hydrophilidae (Hydrochus)</b> (p. 617)
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147(125).	Fore coxal cavities externally open (Fig. 35.15O) .....	148
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149(148).	Mesepisterna distinctly separated at midline, the distance between them more than 0.25 times mid coxal width (Fig. 35.6B); all ventrites free; upper surfaces glabrous or subglabrous .....	<b>Salpingidae-SALPINGINAE</b> (pt, p. 669)
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150(149).	Body less than 4 times as long as wide and not strongly flattened (Fig. 35.54H) .....	<b>Mycteridae-LACCONOTINAE</b> (p. 668)
	Body more than 4 times as long as wide and strongly flattened (Fig. 35.54I) .....	<b>Mycteridae (Hemipeplus)</b> (p. 668)
151(148).	Antennal insertions exposed from above (Figs 35.15B–D) .....	152
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152(151).	Hind trochanter less than 2 times as long as wide, with strongly oblique femoral attachment (Fig. 35.6B); transverse occipital ridge or carina absent; upper surfaces glabrous or subglabrous, clothed with a few minute setae only .....	153
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153(152).	Mid coxae separated by less than width of one coxa; intercoxal process of prosternum not expanded at apex (Fig. 35.15O) .....	<b>Salpingidae-SALPINGINAE</b> (pt, p. 669)
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154(151).	Body ovate; base of prothorax as broad as combined elytral bases; eyes large, almost meeting dorsally; antennae fitting into cavities on pronotal hypomera; upper surfaces smooth and subglabrous .....	<b>Monommidae</b> (p. 664)
	Body more elongate; base of prothorax distinctly narrower than combined elytral bases; eyes small and well separated; pronotal hypomera without antennal cavities; upper surfaces usually tuberculate or costate and clothed with scale-like setae .....	<b>Zopheridae</b> (pt, p. 664)
155(147).	Antennal segments 10; head with rostrum which is longer than it is broad (Fig. 35.57D); pronotum with 3 longitudinal grooves .....	<b>Salpingidae (Tretothorax)</b> (p. 669)
	Antennal segments 11; head without elongate rostrum; pronotum without longitudinal grooves .....	156
156(155).	Intercoxal process of prosternum not or only slightly, gradually expanded at apex (Fig. 35.15Q) .....	<b>Tenebrionidae</b> (pt, p. 665)
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157(156).	Antennae fitting into grooves on pronotal hypomera; all coxae moderately to widely separated; length more than 20 mm; dorsal surfaces tuberculate .....	<b>Zopheridae (Zopherosis)</b> (p. 664)
	Antennae not fitting into hypomeral grooves; fore coxae and hind coxae contiguous; length less than 5 mm; dorsal surfaces not tuberculate .....	<b>Salpingidae (Elacatis)</b> (p. 669)
158(21).	Tarsal segments on hind leg at least as many as on mid leg .....	159
	Tarsal segments on hind leg 1 less than on mid leg; abdomen usually with only 4 ventrites, or if 5 are present, then the suture between the first 2 is weak or incomplete; length rarely exceeding 3.5 mm .....	<b>Aderidae</b> (pt, p. 671)
159(158).	Head without elongate rostrum .....	160
	Head with rostrum which is longer than it is broad (Figs 35.61A, C, D) .....	180

- 160(159). Antennae without a distinct club (sometimes gradually clavate) (Figs 35.46H, 59, 61D) ..... 161  
 Antennae with a distinct club consisting of from 1 to 7 segments (Figs 35.48A–D, 61A, B, 62J) ..... 171
- 161(160). Mesepisterna distinctly separated at midline, the distance between them more than 0.25 times mid coxal width (Fig. 35.6B) ..... 162  
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- 162(161). Posterior edge of hind coxa excavate, coxal plate partly concealing base of femur in repose (Fig. 35.36B); lateral pronotal carinae well-developed posteriorly but obsolete anteriorly; posterior edge of pronotum finely crenulate with 4 excavations; scutellum deeply notched anteriorly; tibial spurs pubescent; antennal segments 4–10 of male with articulated appendages ..... **Ptilodactylidae**-PTILODACTYLINAE (p. 635)  
 Posterior edge of hind coxa not excavate, base of hind femur not concealed in repose (Fig. 35.59B); without other characters in combination ..... 163
- 163(162). Mandibles without dorsal tubercles; hind trochanter with strongly oblique femoral attachment (Fig. 35.6B) ..... 164  
 Mandibles each with dorsal tubercle (Fig. 35.15E); hind trochanter with transverse or slightly oblique femoral attachment (Fig. 35.46D) ..... **Boganiidae** (pt, p. 650)
- 164(163). Intercoxal process of prosternum incomplete, terminating between coxae (Fig. 35.15O); head strongly deflexed and prothorax narrowed anteriorly, with incomplete lateral carinae (Fig. 35.59A); hind femur inflated, with 1 or more teeth on inner edge; tarsal claws toothed ..... **Chrysomelidae**-BRUCHINAE (p. 674)  
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- 165(164). Antennal scape less than 3 times as long as pedicel ..... 166  
 Antennal scape more than 3 times as long as pedicel ..... 170
- 166(165). Mid coxal cavities open laterally (partly closed by mesepimeron) (Figs 35.15T–V) ..... 167  
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- 167(166). Antennal insertions exposed from above (Fig. 35.15B) ..... **Chrysomelidae** (pt, p. 674)  
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- 168(167). Lateral pronotal carinae complete and sharply defined (Fig. 35.15R); labrum visible; fore coxae externally globular and not projecting below prosternum; fore and mid coxal cavities moderately to widely separated, by more than 0.4 times coxal width ..... **Silvanidae**-SILVANINAE (pt, p. 651)  
 Lateral pronotal carinae absent; labrum not visible; fore coxae externally globular to conical and projecting well below prosternum (Fig. 35.15X); fore coxal cavities contiguous or subcontiguous; mid coxal cavities narrowly separated, by less than 0.4 times coxal width ..... **Belidae** (pt, p. 679)
- 169(166). Ventrites 1–4 connate; head usually produced anteriorly forming short rostrum; maxillae usually reduced and partly concealed by genal projections; lateral pronotal carinae distinct posteriorly but absent anteriorly ..... **Anthribidae** (pt, p. 679)  
 All ventrites free or first 2 connate (2 or 3 sub-basal ventrites connate in some *Cryptocephalinae*); head without rostrum; maxillae well developed and not concealed by genal projections; lateral pronotal carinae usually complete or absent ..... **Chrysomelidae** (pt, p. 674)
- 170(165). Antennae not borne on raised tubercles; antennae usually less than two-thirds as long as body ..... **Chrysomelidae** (pt, p. 674)  
 Antennae borne on raised tubercles (Figs 35.58A, B); antennae usually more than two-thirds as long as body ..... **Cerambycidae** (pt, p. 672)
- 171(160). Mid coxal cavities open laterally (partly closed by mesepimeron) (Figs 35.15T–V) ..... 172  
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- 172(171). Pronotum without callosities at anterior angles; mandibles without dorsal tubercles ..... 173  
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- 173(172). Fore coxae externally transverse and not projecting below prosternum (Fig. 35.15M) ..... **Nitidulidae** (pt, p. 649)  
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- 174(171). Fore coxal cavities externally open (Figs 35.15J–O) ..... 175  
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- 175(174). Body very short and broad, less than 1.5 times as long as wide; fore coxal cavities narrowly separated, by less than 0.4 times coxal width; tarsal claws toothed or appendiculate (Fig. 35.59G) ..... **Phalacridae** (p. 653)  
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 Frontoclypeal suture absent or indistinct; antennal club not flattened; body less than 3 times as long as wide or densely pubescent; coloration different ..... **Languriidae**-XENOSCELINAE (pt, p. 654)
- 177(174). Lateral pronotal carinae complete and sharply defined (Fig. 35.48E); apical segment of maxillary palp well devel-



- oped and slightly to strongly expanded at apex (Figs 35.15A, B) ..... **Erotylidae**-TRIPLACINAE (p. 654)
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- 178(177). Labrum free and mostly visible; antennal scape less than 3 times as long as pedicel; antennae not geniculate; ventrites 1 to 4 connate ..... **Anthribidae** (pt, p. 679)
- Labrum entirely or almost entirely concealed beneath clypeus or solidly fused to clypeus (apparently absent); antennal scape more than 3 times as long as pedicel; antennae geniculate (Fig. 35.62J); ventrites 1 and 2 connate ... 179
- 179(178). Outer edge of mid tibia simple ..... **Curculionidae** (pt, p. 682)
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- 180(159). Antennal segments 11 (or rarely more) ..... 181
- Antennal segments fewer than 11 ..... 190
- 181(180). Labrum free and mostly visible (Figs 35.15A–D) ..... 182
- Labrum entirely or almost entirely concealed beneath clypeus or solidly fused to clypeus (apparently absent) .... 183
- 182(181). Mid coxal cavities narrowly separated, by less than 0.4 times coxal width; all ventrites free; pronotum without a trace of lateral carinae ..... **Nemonychidae** (p. 678)
- Mid coxal cavities moderately to widely separated, by more than 0.4 times coxal width (Fig. 35.48J); ventrites 1 to 4 connate; pronotum almost always with lateral carinae (sometimes indistinct or very short) ..... **Anthribidae** (pt, p. 679)
- 183(181). Antennae without a distinct club (sometimes gradually clavate) (Fig. 35.15A); elytra more than 2 times as long as wide ..... 184
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- 184(183). Mid coxal cavities open laterally (partly closed by mesepimeron) (Figs 35.15T–V); ventrites 1 and 2 free and not or only slightly longer than 3, 4 or 5; head not abruptly constricted posteriorly ..... **Belidae** (pt, p. 679)
- Mid coxal cavities distinctly closed laterally by meeting of mesosternum and metasternum (Fig. 35.15W); ventrites 1 and 2 strongly connate or completely fused (with suture between them incomplete or absent) and much longer than 3, 4 or 5; head abruptly constricted posteriorly to form neck ..... **Brentidae**-BRENTINAE (p. 680)
- 185(183). Body narrowly elongate, more than 3 times as long as wide ..... 186
- Body less than 3 times as long as wide ..... 187
- 186(185). Antennal scape less than 3 times as long as pedicel; antennae not geniculate ..... **Brentidae**-EURHYNCHINAE (p. 680)
- Antennal scape more than 3 times as long as pedicel; antennae geniculate (Fig. 35.62I) ..... **Curculionidae** (pt, p. 682)
- 187(185). Hind trochanter less than 2 times as long as wide, with strongly oblique femoral attachment (Fig. 35.6B) ..... 188
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- 189(188). Antennal insertions exposed from above; ventrites 1 to 3 or 4 strongly connate ..... **Attelabidae** (*Euops* and *Auletobius*) (p. 680)
- Antennal insertions concealed from above; all ventrites apparently free ..... **Attelabidae** (*Car*) (p. 680)
- 190(180). Antennal scape less than 3 times as long as pedicel; antennae not geniculate; antennae 10-segmented with a 1-segmented antennal club, which is more than 5 times as long as wide ..... **Brentidae** (*Cylas*) (p. 680)
- Antennal scape more than 3 times as long as pedicel; antennae geniculate (Fig. 35.62I); antennal club less than 4 times as long as wide ..... 191
- 191(190). Hind trochanter more than 2 times as long as wide, with transverse or slightly oblique femoral attachment (Fig. 35.47L); antennae 9-segmented with a loose, 3-segmented club ..... **Brentidae** (*Nanophyes*) (p. 680)
- Hind trochanter less than 2 times as long as wide, with strongly oblique femoral attachment (Fig. 35.6B); antennal club compact (Figs 35.62G, J, M, O) ..... **Curculionidae** (pt, p. 682)
- 192(21). Fore trochantins at least partly exposed (Figs 35.15J–M) or mouth-parts directed ventrally or posteriorly ..... 193
- Fore trochantins completely concealed or apparently absent (Figs 35.15N–S); mouth-parts directed anteriorly (although head may be somewhat declined) ..... 201
- 193(192). First 3 tarsal segments expanded and ventrally pilose, the 3rd deeply bilobed (Figs 35.59I, J); mouth-parts directed ventrally or posteriorly; body more than 2 times as long as wide or head much narrower than base of pronotum; antennal insertions approximate; length greater than 3 mm ..... **Chrysomelidae**-HISPINAE (p. 674)
- If first 3 tarsal segments ventrally pilose, 3rd not deeply bilobed, head almost as wide as base of pronotum, and length less than 2 mm; mouth-parts directed anteriorly (although head may be declined); antennal insertions well separated ..... 194
- 194(193). Antenna with 7 segments and a loose, 3-segmented club preceded by pubescent cupule; head visible from above (Fig. 35.23A); body usually covered with debris ..... **Hydrophilidae** (*Spercheus*) (p. 617)
- Antenna with 8 or 9 segments and a loose, 5- or 6-segmented club preceded by glabrous cupule (Figs 35.25A, B);

- head visible from above ..... **Hydraenidae** (pt, p. 619)
- Antenna with 7 to 10 segments and a compact, 1- to 3-segmented club with no cupule; head strongly deflexed and not visible from above ..... 195
- Antenna with 11 segments and if clubbed, without cupule ..... 196
- 195(194). Hind coxae contiguous, with large plates concealing femora (Fig. 35.28E); elytra very finely punctate, smooth and shiny (Fig. 35.28D); antennae 10-segmented with a 2-segmented club ..... **Clambidae** (p. 625)
- Hind coxae widely separated, without plates; elytra coarsely punctate, costate and dull (Figs 35.23B, C); antennae 7- or 9-segmented with 1- or 3-segmented club ..... **Hydrophilidae** (*Georissus*) (pt, p. 617)
- 196(194). Antennae much shorter than head width, incrassate or with last 7 segments expanded forming weak club (Fig. 35.36C); body more than 2 times as long as wide, somewhat flattened and pubescent; fore tibiae with long spines on outer edge ..... **Heteroceridae** (p. 634)
- Antennae with a distinct club consisting of 1 to 5 segments (Figs 35.36B, 51A, B); if antennae slightly shorter than head width, body less than 1.5 times as long as wide, strongly convex and glabrous ..... 197
- 197(196). Antennal club not 5-segmented or with 2nd segment subequal to or larger than 1st; fore coxae externally transverse and not projecting below prosternum (Fig. 35.15I) ..... 198
- Antennal club 5-segmented with 2nd segment smaller than 1st or 3rd (Figs 35.25C, D); fore coxae externally globular to conical and projecting well below prosternum (Figs 35.15H, K, O) ..... **Leioididae** (pt, p. 619)
- 198(197). Mid coxal cavities contiguous or subcontiguous (Fig. 35.15W); mesosternum without cavity ..... 199
- Mid coxae moderately to widely separated, by more than 0.4 times (usually more than 1) coxal width; mesosternum with distinct cavity into which apex of prosternal process is inserted (Fig. 35.15U) ..... 200
- 199(198). Body very short and broad, less than 1.5 times as long as wide, strongly convex and glabrous; hind coxae moderately to very widely separated; mid tarsi with lobed segments (Fig. 35.15AA) ... **Nitidulidae** (*Cybocephalus*) (p. 649)
- Body more than 1.5 times as long as wide, slightly to strongly flattened and densely setose; hind coxae contiguous or narrowly separated; mid tarsi without lobed segments ..... **Mycetophagidae** (pt, p. 660)
- 200(198). Hind coxae transverse and narrowly separated, with complete, transverse coxal plates (Fig. 35.36B); all tibiae spinose; transverse occipital ridge or carina present (Fig. 35.15F); elytra with distinct puncture rows; eyes lateral and well separated; vestiture of scale-like setae ..... **Byrrhidae** (*Microchaetes*) (p. 634)
- Hind coxae subglobular and widely separated, without coxal plates; tibiae not spinose; transverse occipital ridge absent; elytral punctation fine and confused; eyes lateral and well separated; vestiture of fine, decumbent hairs ..... **Limnichidae** (*Hyphalus*) (p. 634)
- Hind coxae large and oblique, approximate, with well-developed, longitudinal coxal plates; only hind tibiae spinose; transverse occipital ridge absent; elytral punctation fine and confused; eyes dorsal and approximate; vestiture of fine, decumbent hairs ..... **Limnichidae** (*Pseudeucinetus*) (p. 634)
- 201(192). Ventrites 5 ..... 203
- Ventrites 6 ..... 202
- 202(201). Antennae 4-segmented; body length greater than 2.5 mm ..... **Endomychidae** (*Trochoideus*) (p. 657)
- Antennae with more than 8 segments; body length less than 2 mm ..... **Corylophidae** (pt, p. 658)
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- 204(203). Antennal insertions exposed from above (Fig. 35.15B) ..... 205
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- 205(204). Intercoxal process on ventrite 1 acute to narrowly rounded (Fig. 35.47L); mid coxal cavities narrowly separated, by less than 0.4 times coxal width ..... 206
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- Body oblong to elongate, more than 1.5 times as long as wide and usually setose (Fig. 35.48G); antenna with 2-segmented, compact club; tarsi and tarsal claws simple ..... **Bothrideridae** (*Teredolaemus*, *Xylariophilus*) (p. 656)
- 207(205). Posterior edge of ventrite 5 simple; frontoclypeal suture distinct (Fig. 35.15A); maxillary palps with apical segment not or only slightly narrower than and usually longer than penultimate segment ..... 208
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- 208(207). Antennal club 1-segmented; ventrite 1 with 1 pair of curved femoral lines (Fig. 35.49D); transverse occipital ridge or carina present (Fig. 35.15F); metasternal longitudinal suture moderately to very long (more than 0.25 times as long as body of sternite) (Fig. 35.49D); prothorax with pair of cavities at anterior angles ..... **Cerylonidae** (*Murmidius*) (p. 656)
- Antennal club 3-segmented; ventrite 1 without femoral lines; transverse occipital ridge or carina absent; metasternal longitudinal suture absent; prothorax without cavities at anterior angles ..... **Endomychidae** (pt, p. 657)
- 209(204). Antennal segments 11 (or rarely more) ..... 210
- Antennal segments fewer than 11 ..... 214
- 210(209). Intercoxal process of prosternum not or only slightly, gradually expanded at apex (Figs 35.15J, M, Q) ..... 211

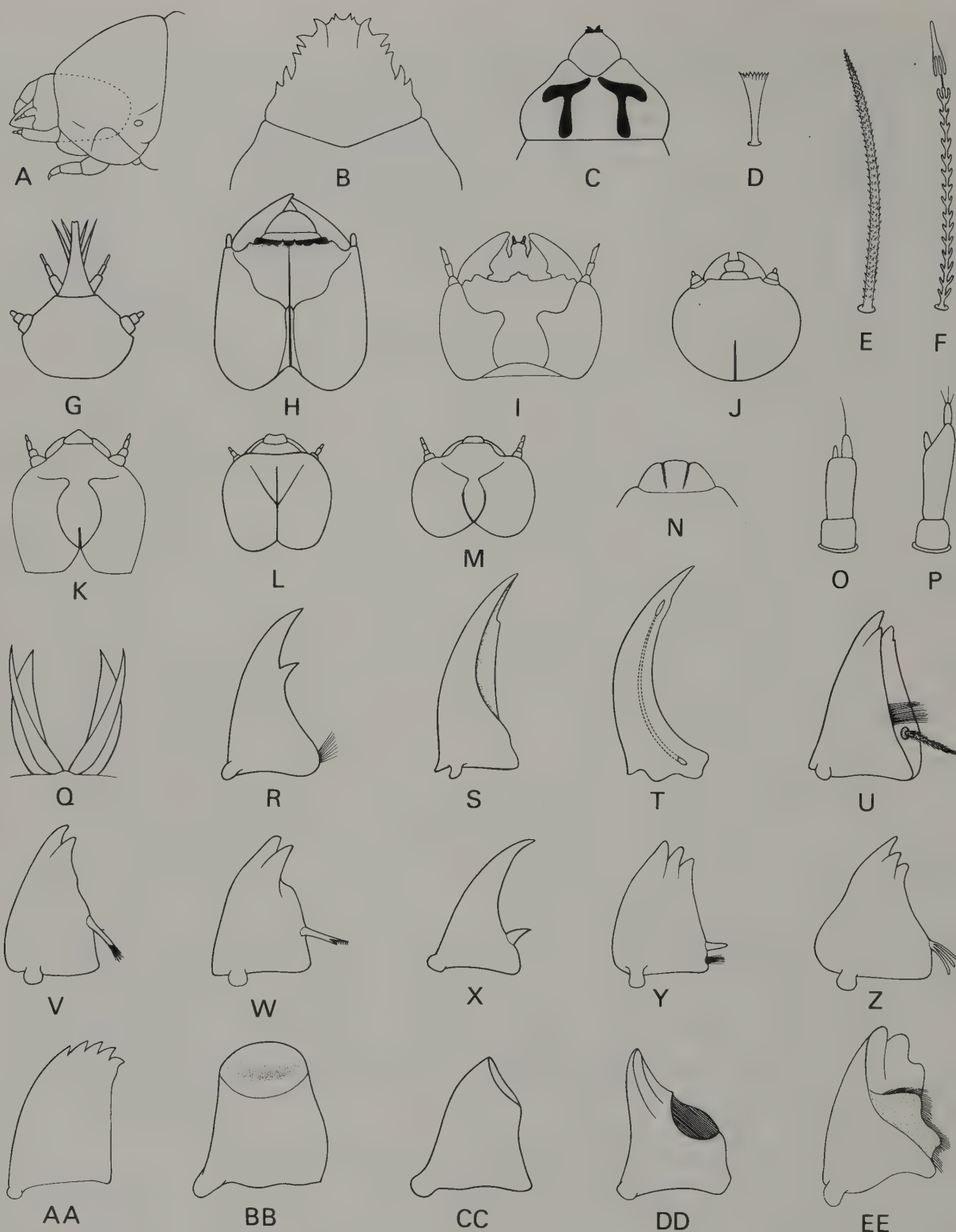


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- 212(211). Body more or less parallel-sided, glabrous, and less than 2 mm long; frontoclypeal suture absent; eyes absent; mid coxal cavities distinctly closed laterally by meeting of mesosternum and metasternum (Fig. 35.15W) ..... **Salpingidae** (*Aglenus*) (p. 669)
- Body ovoid to oblong and densely setose; eyes present; mid coxal cavities open laterally (partly closed by mesepimeron) (Figs 35.15T–V), or if laterally closed, then frontoclypeal suture present and length more than 2 mm ..... **Mycetophagidae** (pt, p. 660)
- 213(210). Antennae with segments 3 to 8 greatly expanded and clothed with scale-like hairs, so that the compact, 3-segmented club is not easily distinguished from the preceding segments; elytra costate and with rows of deep window punctures; body clothed in scale-like hairs and often covered with debris ..... **Colydiidae** (*Orthocerus*) (p. 664)
- Antennae without expanded segments or scale-like hairs, with relatively loose, 3-segmented club; body surfaces smooth and subglabrous ..... **Salpingidae** (*Ocholissa*) (p. 669)
- 214(209). Mid coxal cavities open laterally (partly closed by mesepimeron) (Figs 35.15T–V); frontoclypeal suture distinct (Fig. 35.15A) ..... **Ciidae** (p. 660)
- Mid coxal cavities distinctly closed laterally by meeting of mesosternum and metasternum (Fig. 35.15W); frontoclypeal suture absent or indistinct ..... **Colydiidae** (pt, p. 664)
- 215(203). Mid coxal cavities open laterally (partly closed by mesepimeron) (Figs 35.15T–V) ..... 216
- Mid coxal cavities distinctly closed laterally by meeting of mesosternum and metasternum (Fig. 35.15W) ..... 218
- 216(215). Antennal segments 11; hind coxae contiguous or very narrowly separated; apical segment of maxillary palp slightly to strongly expanded at apex (Fig. 35.15A); fore coxal cavities internally open (Fig. 35.15S) ..... **Zopheridae** (*Meryx*) (p. 664)
- Antennal segments fewer than 11; hind coxae moderately to widely separated (Fig. 35.48J); apical segment of maxillary palp cylindrical to fusiform (Fig. 35.15E); fore coxal cavities internally closed (Figs 35.15Q, R) ..... 217
- 217(216). Elytra concealing abdominal tergites or exposing apex of one only; antennal insertions concealed from above by projections of the frons (Fig. 35.15A); ventrite 1 with 1 pair of straight femoral lines (Fig. 35.48J) ..... **Tenebrionidae** (*Euclarkia*, *Kershawia*) (p. 665)
- Elytra exposing most of one abdominal tergite (Fig. 35.46G); antennal insertions exposed from above (Fig. 35.15B); ventrite 1 without femoral lines ..... **Rhizophagidae** (pt, p. 650)
- 218(215). Antennal insertions exposed from above (Fig. 35.15B) ..... 219
- Antennal insertions concealed from above by projections of the frons (Fig. 35.15A) ..... 223
- 219(218). Lateral pronotal carinae complete and sharply defined (Fig. 35.48I) ..... 220
- Lateral pronotal carinae incomplete anteriorly or absent (Fig. 35.55A) ..... 222
- 220(219). Posterior edge of ventrite 5 simple; maxillary palps with apical segment not or only slightly narrower than and usually longer than penultimate segment ..... 221
- Posterior edge of ventrite 5 crenulate (Fig. 35.15BB); maxillary palps with apical segment much narrower than and usually shorter than penultimate segment (Fig. 35.48L) ..... **Cerylonidae** (*Australiorylon*) (p. 656)
- 221(220). Antennae 11-segmented; body narrowly elongate, more than 3 times as long as wide; prosternum in front of coxae longer than intercoxal process (Fig. 35.48J); ventrites 3 and 4 without lateral projections ..... **Bothrideridae**-**BOTHRIDERINAE** (p. 656)
- If antennae 11-segmented, body less than 3 times as long as wide; if body elongate and prosternum in front of coxae longer than intercoxal process, antennae 10-segmented and ventrites 3 and 4 with lateral projections extending beneath elytral epipleura ..... **Cerylonidae**-**EUXESTINAE**, **METACERYLONINAE** (p. 656)
- 222(219). Antennal club 2-segmented; mid coxae separated by less than width of one coxa; intercoxal process of prosternum not or only slightly, gradually expanded at apex (Fig. 35.15Q) ..... **Colydiidae** (*Nematidium*) (p. 664)
- Antennal club 3-segmented; mid coxae separated by more than width of one coxa (Fig. 35.48J); intercoxal process of prosternum strongly and usually abruptly expanded at apex ..... **Prostomidae** (p. 667)
- 223(218). Pre-gular area with pair of laterally-opening, setose cavities; transverse occipital ridge or carina present (Fig. 35.15F); metasternum with femoral lines behind mid coxal cavities; first 2 segments of mid tarsus with membranous, setose lobes beneath (Fig. 35.15Z) ..... **Biphyllidae** (pt, p. 654)
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- 224(223). All ventrites free (overlapping and similarly articulated, often with exposed connecting membrane) ..... 225
- With at least first 3 ventrites connate (abutting one another, not overlapping, and without exposed connecting membrane) (Fig. 35.6B) ..... 226
- 225(224). Body shorter and broader, less than 3 times as long as wide; pronotum produced anteriorly over head; antennae 10-segmented with 1-segmented club; metasternum subequal to or shorter than first ventrite; body clothed with flat, silvery-white scales (Fig. 35.44G) ..... **Phycosecidae** (p. 647)

- Body elongate, more than 3 times as long as wide; pronotum not produced anteriorly over head; antennae 11-segmented with 3-segmented club; metasternum distinctly longer than first ventrite; body clothed with fine setae ..... **Cleridae**-**THANEROCLERINAE** (p. 645)
- 226(224). Ventrites 3 and 4 not overlapping and without exposed connecting membrane between them; elytral epipleura absent, very narrow or more or less vertical; antennae usually 11-segmented with a 2-segmented club or 10-segmented with a 1-segmented club (if club 4- or 5-segmented, then body more than 5 times as long as wide) ..... **Colydiidae** (pt, p. 664)
- Ventrites 3 and 4 overlapping and with exposed connecting membrane between them (Fig. 35.6B); elytral epipleura well-developed, at least basally, and horizontal; antennae 7-segmented with a 1-segmented club, 10-segmented with a 2-segmented club or 11-segmented with a 4- or 5-segmented club (in which case body less than 3 times as long as wide) ..... **Tenebrionidae** (pt, p. 665)
- 227(21). Head not concealed by prothorax ..... 228
- Head very small and almost or entirely concealed by prothorax (Figs 35.49F, G, I) ..... **Corylophidae** (pt, p. 658)
- 228(227). Ventrite 1 without femoral lines; frontoclypeal suture present (Fig. 35.15A); apical segment of maxillary palp cylindrical to fusiform, not expanded at apex (Fig. 35.15E); pronotum usually with paired basal impressions, basal carinae or submarginal carinae (Fig. 35.49A) ..... **Endomychidae** (pt, p. 657)
- Ventrite 1 with 1 pair of curved femoral lines (Fig. 35.49D); frontoclypeal suture absent; apical segment of maxillary palp slightly to strongly expanded and truncate at apex (Figs 35.49B–D) (except in a few species which are less than 2 mm long); pronotum without paired impressions or carinae ..... **Coccinellidae** (pt, p. 658)
- 229(21). Fore trochantins at least partly exposed (Fig. 35.3C); mid coxal cavities open laterally (partly closed by mesepimeron) (Fig. 35.15T); hind coxae contiguous or narrowly separated (Fig. 35.28E) ..... 230
- Fore trochantins completely concealed or apparently absent (Figs 35.15O, Q); mid coxal cavities distinctly closed laterally by meeting of mesosternum and metasternum (Fig. 35.15W); hind coxae moderately to very widely separated (Fig. 35.48J) ..... 231
- 230(229). Antennal club 3-segmented; mid coxae separated by more than width of one coxa (Fig. 35.48J); ventrites 3 ..... **Microsporidae** (p. 608)
- Antennal club 5-segmented with 2nd segment smaller than 1st or 3rd (Figs 35.25C, D); mid coxae separated by less than width of one coxa; ventrites 5 or 6 ..... **Leiodidae** (pt, p. 619)
- 231(229). Fore coxal cavities externally open (Figs 35.15M, O) ..... 232
- Fore coxal cavities externally closed (Figs 35.15Q, R) ..... 239
- 232(231). Body minute (less than 1 mm long) and narrowly elongate (about 4 times as long as wide); metasternum distinctly longer than abdomen ..... **Jacobsoniidae**-**DEROLATHRINAE** (p. 641)
- Without above combination of characters ..... 233
- 233(232). Pronotum constricted at base, with paired longitudinal grooves joined by transverse impression; antennal club 1- or 2-segmented; ventrites 6 ..... **Endomychidae** (*Holoparamesus*) (p. 657)
- Pronotum not constricted at base, if paired basal grooves present, then antennal club 3-segmented; ventrites 5 ... 234
- 234(233). Posterior edge of ventrite 5 crenulate (Fig. 35.15BB); labrum strongly narrowed and acute apically, forming a sucking tube (Fig. 35.48L) ..... **Cerylonidae** (*Cautomus*) (p. 656)
- Posterior edge of ventrite 5 simple; labrum not strongly narrowed, not forming part of sucking tube ..... 235
- 235(234). First 3 ventrites solidly fused (Fig. 35.6B); base of pronotum distinctly narrower than combined elytral bases; antennae 10-segmented, with segments 3–9 strongly transverse and segment 10 enlarged, truncate and densely setose at apex only; length greater than 3.5 mm ..... **Colydiidae** (*Rhopalocerus*) (p. 664)
- All ventrites free; if base of pronotum narrower than combined elytral bases, antennal club 3-segmented; antennae differently formed; length less than 3 mm ..... 236
- 236(235). Body narrowly elongate, more than 3 times as long as wide; eyes absent ..... **Bothrideridae** (*Anommatus*) (p. 656)
- Body shorter and stouter, less than 2 times as long as wide; eyes present ..... 237
- 237(236). Antennal insertions concealed from above by frons; frontoclypeal suture present (Fig. 35.15A); antennae 8-segmented with 1-segmented club; eyes reduced (with fewer than 10 facets) ..... **Endomychidae** (*Displotera*) (p. 657)
- Antennal insertions exposed from above; if frontoclypeal suture present, antennal club 3-segmented; eyes well developed ..... 238
- 238(237). Frontoclypeal suture absent; ventrite 1 with pair of curved femoral lines (Fig. 35.49D); antennae short and stout, incrassate or with 1-segmented club (Fig. 35.49B) ..... **Coccinellidae**-**STICHOLOTIDINAE** (p. 658)
- Frontoclypeal suture present (Fig. 35.15A); ventrite 1 without curved femoral lines; antennae longer, with distinct, 3-segmented club (Fig. 35.49A) ..... **Endomychidae**-**MYCHOTHENINAE** (p. 657)
- 239(231). Lateral pronotal carinae absent; metasternum longer than abdomen; antennal segments 2 to 10 transverse and bearing ring of scale-like setae at apex (Fig. 35.41) ..... **Jacobsoniidae** (*Sarothrias*) (p. 641)
- Lateral pronotal carinae complete and sharply defined; metasternum shorter than abdomen; antennae without scale-like hairs ..... 240
- 240(239). Posterior edge of ventrite 5 simple ..... 241
- Posterior edge of ventrite 5 crenulate (Fig. 35.15BB) ..... **Cerylonidae** (*Cerylonopsis*) (p. 656)
- 241(240). Antennal club 2- or 3-segmented; mid coxae separated by less than width of one coxa; body more than 1.5 times as long as wide, with pronotum narrower at base than elytra (Fig. 35.49K) ..... **Lathridiidae** (p. 660)
- Antennal club 1-segmented; mid coxae separated by more than width of one coxa; body very short and broad, less



- than 1.5 times as long as wide, almost circular in outline (Fig. 35.49E) ..... **Discolomidae** (p. 656)
- 242(20). Tarsal segments on hind leg at least as many as on mid leg ..... 243
- Tarsal segments on hind leg 1 fewer than on mid leg ..... 255
- 243(242). Antennae without a distinct club (sometimes gradually clavate) (Fig. 35.15A) ..... 244
- Antennae with a distinct club consisting of from 1 to 7 segments (Figs 35.25F, 26B, 46F) ..... 252
- 244(243). Mesepisterna distinctly separated at midline, the distance between them more than 0.25 times mid coxal width (Fig. 35.6B); hind wing with normal transverse folds and usually folded beneath elytra ..... 245
- Mesepisterna broadly joined at midline, so that mesosternum is separated from anterior edge of mesothorax (Fig. 35.15v); hind wing lacking transverse folds and almost completely exposed by minute elytra (Fig. 35.43A) ..... **Lymexylidae** (*Atractocerus*) (p. 644)
- 245(244). Tarsus of mid leg with 5 distinct segments ..... 246
- Tarsus of mid leg pseudotetramerous (with 4 distinct segments plus a highly reduced penultimate segment, concealed by lobe of preceding segment) (Fig. 35.59F) ..... **Cerambycidae** (pt, p. 672)
- Tarsus of mid leg with 4 distinct segments ..... **Staphylinidae** (pt, p. 621)
- Tarsus of mid leg with 3 distinct segments (or rarely fewer) ..... 251
- 246(245). All tarsi with at least 1 segment lobed beneath; metasternal longitudinal suture present, or if indistinct, then tarsal claws toothed or pectinate ..... 247
- Tarsal segments simple, not lobed beneath; metasternal longitudinal suture absent; tarsal claws simple ..... **Staphylinidae** (pt, p. 621)
- 247(246). Antennal insertions laterally situated and not visible from above; labrum completely concealed; prosternal process laminate but complete (Fig. 35.15K); tarsal claws pectinate (with more than 1 tooth); antennae gradually expanded and flattened apically ..... **Cleridae** (*Cylidrus*) (p. 645)
- Antennal insertions dorsally situated and exposed (Fig. 35.15B); labrum at least partly exposed; prosternal process incomplete or absent (Fig. 35.15L); tarsal claws simple or with 1 tooth only; antennae filiform, serrate or pectinate ..... 248
- 248(247). Antennal insertions approximate, the distance between them less than or only slightly greater than the diameter of one of them (Figs 35.15C, D) ..... 249
- Antennal insertions moderately to widely separated, the distance between them at least 1.5 times and usually 2 times the diameter of one of them (Fig. 35.15B) ..... 250
- 249(248). Abdomen with luminous organ (visible as yellowish white colour of 5th ventrite) (Fig. 35.38D); apical segment of maxillary palp fusiform (Fig. 35.15D) ..... **Lampyridae** (some females) (p. 640)
- Abdomen without luminous organ; apical segment of maxillary palp slightly to strongly expanded at apex (Figs 35.15A, C) ..... **Lycidae** (some females) (p. 638)
- 250(248). Labrum membranous; tarsal claws simple or weakly toothed at base; vestiture consisting of short, fine hairs; fore tarsus with basal segment normal in both sexes ..... **Cantharidae** (pt, p. 640)
- Labrum sclerotised; tarsal claws strongly toothed at base; vestiture of short, fine hairs mixed with stiff, erect, dark setae; fore tarsus with basal segment enlarged and bearing a fine comb in male ..... **Melyridae-MALACHIINAE** (pt, p. 647)
- 251(245). Abdomen without dorso-ventral flexibility; tarsi usually with 1 claw or 2 very unequal claws; apical segment of maxillary palp much larger than rest and usually variously modified; body often bearing setose foveae (trichomes) at various points (Figs 35.26B, C) ..... **Pselaphidae** (pt, p. 624)
- Abdomen more or less flexible in dorso-ventral plane; tarsi usually with 2 equal claws; apical segment of maxillary palp rarely enlarged and modified; body without trichomes ..... **Staphylinidae** (pt, p. 621)
- 252(243). Fore coxal cavities externally open (Figs 35.15K, L); metasternal longitudinal suture absent; antennal club usually 2-segmented, more than 3-segmented, or not compact ..... 253
- Fore coxal cavities externally closed (Figs 35.15P, Q); metasternal longitudinal suture present (Figs 35.15T, U); antenna with 3-segmented, compact club (Fig. 35.46F) ..... **Nitidulidae** (pt, p. 649)
- 253(252). Antenna with a 3-segmented, loose, symmetrical club, which is finely, densely and uniformly pubescent, and preceded by a strongly transverse, glabrous cup-like segment (Fig. 35.25F); scutellum very large; elytra carinate; length greater than 25 mm ..... **Silphidae** (*Diamesus*) (p. 621)
- Without above combination of characters ..... 254
- 254(253). Abdomen without dorso-ventral flexibility; tarsi with 3 segments or fewer, usually with 1 claw or 2 very unequal claws; apical segment of maxillary palp much larger than rest and usually variously modified; body often bearing setose foveae (trichomes) at various points (Figs 35.26B, C) ..... **Pselaphidae** (pt, p. 624)
- Abdomen more or less flexible in dorso-ventral plane; tarsi usually with more than 3 segments and with 2 equal claws; apical segment of maxillary palp rarely enlarged and modified; body without trichomes ..... **Staphylinidae** (pt, p. 621)
- 255(241). Mid coxal cavities open laterally (partly closed by mesepimeron) (Fig. 35.15T); hind coxae contiguous or very narrowly separated; head abruptly constricted posteriorly to form a broad or narrow neck (Fig. 35.53A); body slightly flattened to moderately convex (Fig. 35.53A) ..... **Rhipiphoridae** (pt, p. 663)
- Mid coxal cavities distinctly closed laterally by meeting of mesosternum and metasternum (Fig. 35.15W); hind coxae moderately to widely separated; head not abruptly constricted posteriorly (sometimes gradually narrowed); body strongly flattened (Fig. 35.57E) ..... **Salpingidae-INOPELINAE** (p. 669)



35.16 Illustrations for larval key (semidiagrammatic). A, prognathous, retracted head. B, Eucnemidae, head of eucnemine type, dorsal. C, Eucnemidae, head and prothorax of melasine type, dorsal. D-F, specialised setae: D, expanded or frayed seta; E, barbed spiciseta; F, hastiseta. G-M, heads, dorsal (anterior, if hypognathous): G, Cerylonidae-Ceryloninae; H, Cerambycidae-Prioninae; I, Elateridae; J, Mordellidae; K, Anthicidae-Anthicinae; L, Chrysomelidae-Galerucinae; M, Salpingidae-Salpinginae. N, curculionid labrum with labral rods. O, P, antennae: O, type with segment 2 truncate; P, staphylinoid type with segment 2 oblique. Q, Lycidae, longitudinally divided mandibles. R-EE, mandibles, ventral: R, Histeridae; S, Cantharidae; T, falcate and perforate type; U, Elmidae; V, Trogossitidae-Trogossitinae; W, Melyridae-Malachiinae; X, Coccinellidae; Y, *Dermestes* sp., Dermestidae; Z, *Litochrus* sp., Phalacridae; AA, Chrysomelidae-Chrysomelinae; BB, Cerambycidae-Cerambycinae; CC, Mordellidae; DD, *Parandra* sp., Cerambycidae-Parandrinae; EE, Erotylidae.

[After Lawrence 1991]



## LARVAE

1. Thoracic legs absent or represented by non-articulated and non-segmented protuberances (pedal lobes), which are broader than long ..... 4  
 Thoracic legs present and articulated at base (or if basal articulation not well defined, then legs segmented or narrow and longer than wide) ..... 2
- 2(1). Labrum partly or entirely (Figs 35.16i, 39κ) fused to head capsule (without or with incomplete clypeolabral suture) ..... 21  
 Labrum entirely free (Figs 35.16j–m) (clypeolabral suture complete) ..... 3
- 3(2). Mandibular mola absent (Figs 35.16q–ee) ..... 81  
 Mandibular mola present (Figs 35.17a–h) ..... 165
- 4(1). Mouth-parts and antennae absent; body very lightly sclerotised and often strongly curved ventrally (C-shaped). Endoparasites of cockroaches ..... **Rhipiphoridae**-RHIPIDIINAE (p. 663)  
 Mouth-parts and antennae present ..... 5
- 5(4). Head protracted or slightly retracted (Figs 35.13a–d) ..... 6  
 Head strongly retracted (Fig. 35.16a) ..... 14
- 6(5). Head highly modified, usually heavily sclerotised, with paired dorsal and ventral endocarinae, or forming wedge-like plate, which is usually apically serrate (Fig. 35.16b); antennae minute, 2-segmented; mandibles either fused to head capsule or with non-opposable, divergent apices; body usually either strongly flattened or with enlarged prothorax bearing paired, longitudinal or T-shaped rods (Fig. 35.16c). In dead wood .... **Eucnemidae** (pt, p. 637)  
 Head capsule of the normal type, without or with a single, median endocarina; mandibles free, with opposable apices; body form different ..... 7
- 7(6). Antennae 1-segmented ..... 8  
 Antennae 2-segmented; mandible with broad base and acute apex; body lightly sclerotised, usually with a deep indentation on each side between meso- and metathorax. Ectoparasites in galleries of ambrosia beetles (**Curculionidae**: **Platypodinae**) ..... **Bothrideridae** (*Sosylus*) (p. 656)  
 Antennae 3-segmented ..... 13
- 8(7). Maxillary palps absent. In nests of wild bees ..... **Meloidae** (pt, p. 668)  
 Maxillary palps 1- or 2-segmented ..... 9  
 Maxillary palps 3-segmented ..... 11
- 9(8). Body straight, somewhat flattened, distinctly tapering posteriorly; head prognathous (Fig. 35.13d), deeply emarginate posteriorly; median endocarina extending anteriorly almost to edge of clypeus. Leaf-miners ..... **Curculionidae** (pt, p. 682)  
 Body usually moderately to strongly curved ventrally (C-shaped) or if straight, then without other characters in combination ..... 10
- 10(9). Labrum with tormae extending from posterolateral angles, but without separate labral rods; mandibular mola (Fig. 35.17f) and hypopharyngeal sclerome (Fig. 35.17z) present. In seeds, dried fruits, and other stored products ..... **Anthribidae** (pt, p. 679)  
 Labral rods present (Fig. 35.16n); mandibular mola absent (Fig. 35.16cc); hypopharyngeal sclerome absent ..... **Curculionidae** and **Brentidae** (pt, pp. 680–2)
- 11(8). Maxilla with galea and lacinia (Fig. 35.17v); maxillary articulating area reduced or absent; abdominal segment 10 with pair of oval lobes separated by longitudinal groove (Fig. 35.18m) ..... **Anobiidae** (pt, p. 643)  
 Maxilla with single mala (Fig. 35.17q); maxillary articulating area well developed; abdominal segment 10 without oval lobes separated by longitudinal groove ..... 12
- 12(11). Frontoclypeal suture absent; mandible with accessory ventral process; apex of mala straight or slightly emarginate, without a lacinial spine on inner edge. In male cones of *Araucaria* and *Agathis* ..... **Nemonychidae** (p. 678)  
 Frontoclypeal suture distinct; mandible without accessory ventral process; apex of mala rounded or acute, with a basal or sub-basal lacinial spine on inner edge. In fungus fruiting bodies, dead wood, stems, vines ..... **Anthribidae** (pt, p. 679)
- 13(7). Median endocarina absent; abdominal apex with respiratory chamber (pocket formed by T8 and T9 and enclosing enlarged 8th spiracles); maxillary palps 4-segmented. In rotting vegetation, leaf litter, dung ..... **Hydrophilidae**-SPHAERIDIINAE (p. 617)  
 Median endocarina located between frontal arms (Fig. 35.16k); abdominal apex without respiratory chamber; maxillary palps 3-segmented. Leaf-miners ..... **Chrysomelidae**-MEGALOPODINAE (p. 674)
- 14(5). Head deeply emarginate posteriorly (Fig. 35.16k). Leaf-miners ..... 15  
 Head not deeply emarginate posteriorly (sometimes with a furrow which houses retractor muscles) ..... 16
- 15(14). Antennae 1-segmented; labral rods present (Fig. 35.16n) ..... **Curculionidae**-Rhynchaenini (p. 682)  
 Antennae with 2 or 3 segments; labral rods absent ..... **Chrysomelidae**-HISPINAE (pt, p. 674)
- 16(14). Antennae 1-segmented; body strongly curved ventrally (C-shaped); maxillary palps 2-segmented; labial palps absent ..... **Anthribidae** (pt, p. 679)  
 Antennae with 2 or 3 segments ..... 17
- 17(16). Spiracles cribriform (Figs 35.18gg, hh); body flattened and prothorax usually much wider than abdomen (Fig. 35.39a), often with a broad tergal plate bearing a pair of impressed rods or a single rod; labial palps absent or



35.17 Illustrations for larval key (semidiagrammatic). A–G, mandibles, ventral: A, Nitidulidae-Cryptarchinae; B, Biphyllidae; C, Rhizophagidae-Monotominae; D, Cucujidae-Cucujinae; E, Languriidae-Xenoscelinae; F, Mycteridae; G, Coccinellidae. H, Pyrochroidae, right and left mandibles in place, dorsal. I–Q, heads, ventral: I, Phalacridae; J, Carabidae; K, Tenebrionidae (left mandible and maxilla removed); L, Salpingidae-Salpinginae; M, Cerambycidae-Prioninae; N, Elateridae; O, Nitidulidae; P, Cantharidae; Q, Chrysomelidae (jagged edge = prothoracic membrane). R, S, ventral mouth-parts (maxillo-labial complex), ventral: R, Limnichidae; S, Callirhipidae. T–Y, maxilla, ventral: T, Leioididae; U, Carabidae; V, Bostrichidae; W, with falciform mala; X, with truncate, cleft mala; Y, Hydrophilidae. Z, Anthicidae-Anthicinae, hypopharynx, dorsal, showing cup-shaped sclerome.

[After Lawrence 1991]



highly reduced. Under bark, in living or dead wood, rarely mining in leaves ..... **Buprestidae** (pt, p. 632)

Spiracles annular or with 1 to several accessory chambers, never cribriform; if labial palps absent, body not flattened ..... 18

18(17). Labial palps absent; maxillary palps 1-segmented; body relatively short and stout; stemmata absent. In seed pods (usually of Fabaceae) ..... **Chrysomelidae-BRUCHINAE** (p. 674)

Labial palps present; maxillary palps with more than 1 segment; body more elongate; stemmata often present ..... 19

19(18). Body relatively straight, not curved ventrally; gular region present (separating labium from thorax) (Fig. 35.17M). Under bark, in living or dead wood ..... **Cerambycidae** (p. 672)

Body strongly curved ventrally (C-shaped) (Fig. 35.13c); gular region absent (labium contiguous with thoracic membrane) (Fig. 35.17Q) ..... 20

20(19). Maxillary palps 3-segmented; labral rods absent; stemmata on each side 3; protergum enlarged and hump-like, with transverse, keeled plate. Boring in twigs and branches ..... **Belidae** (p. 679)

Maxillary palps 2-segmented; labral rods present (Fig. 35.16N); stemmata on each side 1; protergum not enlarged and hump-like. In developing leaves, shoots or flower buds ..... **Attelabidae-RHYNCHITINAE** (p. 680)

21(2). Entire head forming sclerotised, serrate or multidentate, wedge-like plate (Fig. 35.16B); legs and antennae minute; body elongate and parallel-sided, moderately to strongly flattened; spiracles biforous (Fig. 35.18FF). In dead wood ..... **Eucnemidae** (pt, p. 637)

Entire head not forming wedge-like plate ..... 22

22(21). Mesothoracic leg with 5 or fewer segments, including tarsungulus (Figs 35.18B–D) ..... 23

Mesothoracic leg with 6 segments, including single claw or paired claws (Figs 35.18A, 22G, J) ..... 72

23(22). Median endocarina well developed, extending from base of head almost to clypeal region; legs minute, 4-segmented and widely separated; body lightly sclerotised, without urogomphi. In male cones of *Araucaria* ..... **Chrysomelidae-MEGALOPODINAE** (p. 674)

Median endocarina absent or coincident with epicranial stem ..... 24

24(23). Mandibular mola absent (Figs 35.16Q–EE) ..... 25

Mandibular mola present (Figs 35.17A–G) ..... 66

25(24). Maxilla without apical lobes (Fig. 35.17Y) ..... 26

Maxilla with single mala (Figs 35.17I–Q, W–X) ..... 34

Maxilla with separate galea and lacinia (Figs 35.17R, T–V) ..... 65

26(25). First segment of maxillary palp without digitiform appendage ..... 27

First segment of maxillary palp with digitiform appendage (Fig. 35.17Y) (usually described as a galea attached to the palpifer) ..... 30

27(26). Antennae 1- or 2-segmented; head moderately to strongly hypognathous (Fig. 35.13B); endoparasites of cockroaches or in nests of native bees and wasps ..... **Rhipiphoridae-RHIPIDIINAE, RHIPIPHORINAE** (p. 663)

Antennae 3-segmented; head prognathous or slightly declined (Fig. 35.13A) ..... 28

28(27). Abdominal apex without respiratory chamber; stemmata on each side less than 6; 8th abdominal spiracles about the same size as others on abdomen. Usually in leaf litter ..... 29

Abdominal apex with respiratory chamber (pocket formed by T8 and T9 and enclosing enlarged 8th spiracles); stemmata on each side 6. At edges of ponds ..... **Hydrophilidae (Hydrochus)** (p. 617)

29(28). Larvae minute, length usually about 0.5 mm; head with 4 stemmata on each side; body clothed with moderately long, scattered setae, some of which are heavy and spine-like (Fig. 35.53C); without paired dorsal glands ..... **Rhipiphoridae-RHIPIDIINAE (triungulins)** (p. 663)

Larvae larger, length usually more than 1 mm; head with 1 large stemma on each side (Fig. 35.17P); body clothed with very short, fine pubescence, which gives surface a dull appearance; paired dorsal glands present on thoracic terga and T1 to T8 or T9 ..... **Cantharidae** (pt, p. 640)

30(26). Abdominal apex without respiratory chamber ..... 31

Abdominal apex with respiratory chamber (pocket formed by T8 and T9 and enclosing enlarged 8th spiracles). In ponds, lakes, slow-moving streams, leaf litter, and dung ..... **Hydrophilidae** (pt, p. 617)

31(30). T9 without urogomphi ..... 32

T9 with urogomphi (Fig. 35.18J) ..... 33

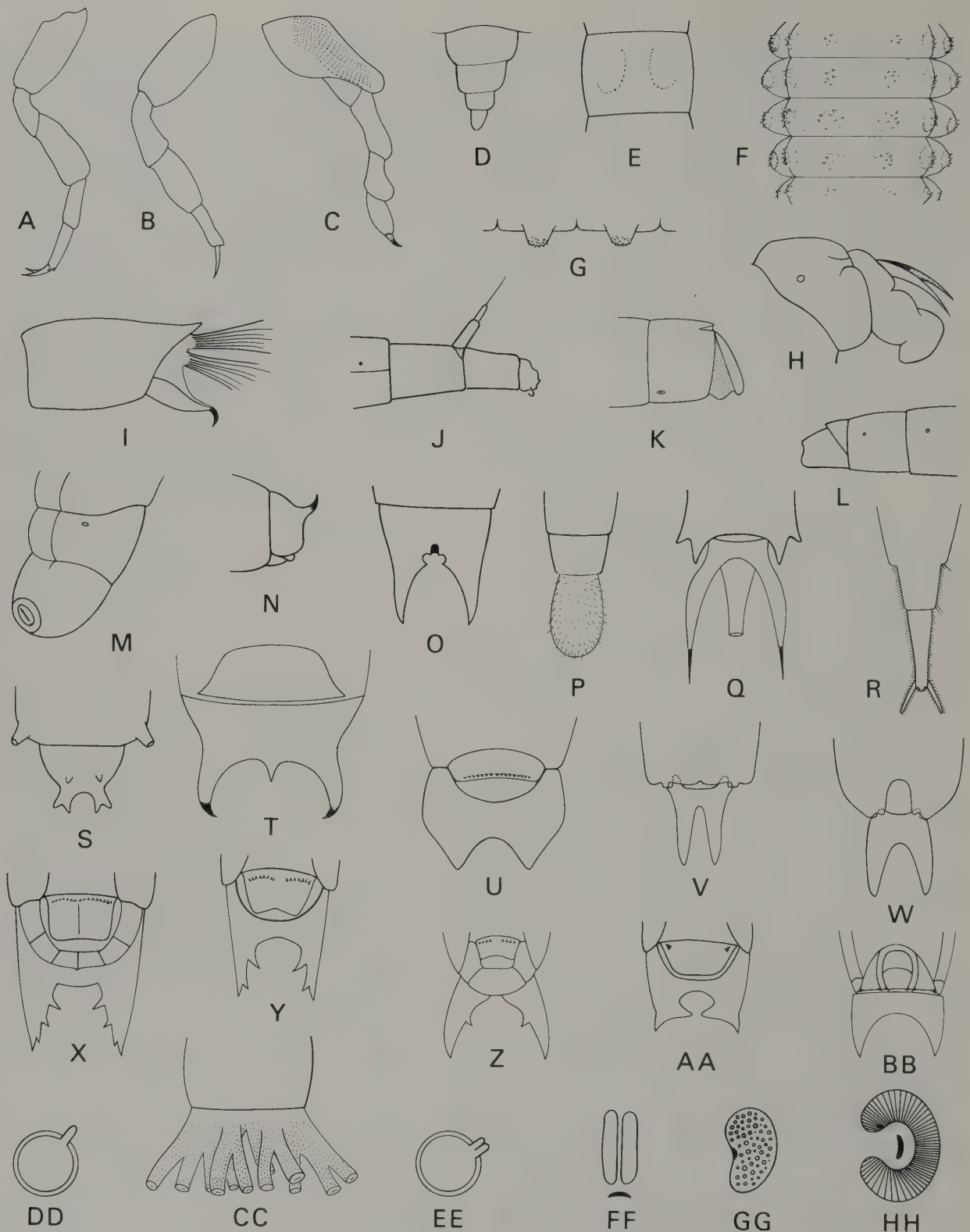
32(31). Mesal surface of mandibular base simple or slightly expanded (Fig. 35.16s); labial palps 2-segmented; maxillary palps 4-segmented; visible abdominal segments 9; stemmata on each side 6; cardo present; abdominal segments 1–7 each with pair of long, narrow, lateral processes (Fig. 35.23H). In ponds ..... **Hydrophilidae-BEROSINAE** (p. 617)

Mesal surface of mandibular base with brush of hairs (penicillus) (Fig. 35.16R); labial palps 3-segmented; maxillary palps 5-segmented; visible abdominal segments 10; stemmata on each side 1 or 0; cardo apparently absent; abdominal segments without long processes. Under bark, in leaf litter, dung, decaying vegetation, ant nests ..... **Histeridae** (pt, p. 618)

33(31). Mesal surface of mandibular base simple or slightly expanded; mesothoracic leg with 3 or 4 segments; urogomphi 1-segmented. In sand or mud along streams ..... **Hydrophilidae (Georissus)** (p. 617)

Mesal surface of mandibular base with brush of hairs (penicillus) (Fig. 35.16R); mesothoracic leg with 5 segments, including tarsungulus (Fig. 35.18B); urogomphi usually with 2 segments ..... **Histeridae** (pt, p. 618)

34(25). Antennae 2-segmented ..... 35



35.18 Illustrations for larval key (semidiagrammatic). A-D, mesothoracic leg: A, Carabidae; B, Polyphaga; C, Lucanidae; D, Mordellidae. E, Phloeostichidae-Hymenoptera, abdominal segment, dorsal. F, Coccinellidae, abdominal terga. G, Oedemeridae, ventral abdominal ampullae or prolegs. H-N, abdominal apex, lateral: H, Chrysomelidae-Donaciinae; I, Elmidae; J, Hydraenidae; K, Callirhipidae; L, Silvanidae-Silvaninae; M, Anobiidae; N, Bothrididae-Bothridinae. O-T, abdominal apex, dorsal: O, Anthicidae-Anthicinae; P, Scaptiidae; Q, Silvanidae-Uleiotaenidae; R, Dytiscidae; S, Nitidulidae-Cryptarchinae; T, Trogossitidae-Lophocaterinae. U-BB, abdominal apex, ventral: U, Prostomidae; V, Phalacridae; W, Laemophloeidae; X, Pythidae; Y, Salpingidae-Othniinae; Z, Salpingidae-Inopeplinae; AA, Salpingidae-Salpinginae; BB, Mycteridae. CC, Lampyridae, abdominal holdfast organ. DD-FF, spiracles: DD, annular-uniforous; EE, annular-biforous; FF, biforous. GG, HH, cribriform spiracles: GG, Trogidae; HH, Scarabaeidae. [After Lawrence 1991]



	Antennae 3-segmented .....	48
	Antennae 4-segmented .....	64
35(34).	T9 without urogomphi .....	36
	T9 with urogomphi (Fig. 35.18N) .....	44
36(35).	Maxillary palps 1-segmented; maxillary and labial palps large and tusk-like; body minute, length less than 1 mm. In bark crevices, soil, in association with cicadas .....	<b>Rhipiceridae</b> (triungulins) (p. 631)
	Maxillary palps 2-segmented .....	37
	Maxillary palps 3-segmented .....	39
	Maxillary palps 4-segmented .....	42
37(36).	Mesal surface of mandibular base simple or slightly expanded; ratio of antennal length to head width more than 0.5; mesothoracic leg with 5 segments, including tarsungulus (Fig. 35.18B); hypostomal rods absent .....	38
	Mesal surface of mandibular base with fixed, rigid, hyaline process, sometimes partly sclerotised (Fig. 35.16X); ratio of antennal length to head width less than 0.15; mesothoracic leg with 3 or 4 segments; hypostomal rods present. In tunnels of wood-boring beetles, in stored products .....	<b>Cucujidae-PASSANDRINAE</b> (pt, p. 651)
38(37).	Body not broadly ovate and strongly flattened; head not concealed from above; dorsal and ventral surfaces similarly sclerotised, yellowish and covered with posteriorly-projecting spines. In tunnels of ambrosia beetles (Curculionidae: Platypodinae) .....	<b>Bothrideridae</b> ( <i>Sosylus</i> triungulins) (pt, p. 656)
	Body broadly ovate, strongly flattened, and disc-like (Figs 35.49H, J); head concealed from above by prothorax; dorsal surfaces much more heavily pigmented or sclerotised than ventral surfaces and clothed with modified setae or scales. In leaf litter .....	<b>Corylophidae</b> (pt, p. 658)
39(36).	Mandibles approximate at base and divided longitudinally, so that 2 pairs of diverging blades or stylets are formed (Fig. 35.16Q). In leaf litter, rotten wood .....	<b>Lycidae</b> (pt, p. 638)
	Mandibles distant at base, converging apically, and not divided longitudinally into 2 parts .....	40
40(39).	Stemmata and epicranial suture absent; antennae geniculate, with a sharp bend in segment 1, and without an obvious sensorium at apex; mandibles highly reduced; abdominal segment 10 forming a slender tube (Fig. 35.27E). In nests of harvester termites ( <i>Drepanotermes</i> ) .....	<b>Staphylinidae</b> ( <i>Drepanoxenus</i> ) (p. 621)
	Stemmata and epicranial suture present; antennae straight and with large sensorium at apex; mandibles well developed; abdominal segment 10 not forming slender tube .....	41
41(40).	Stemmata on each side 1, or 3 forming tight cluster or triangle; antennal sensorium short and dome-like; labial palps separated by more than 2 basal diameters; stipes short and broad; head without protrusible glands. In leaf litter, moss .....	<b>Scydmaenidae</b> (pt, p. 621)
	Stemmata on each side 2 or 3 well separated and forming a row; antennal sensorium elongate, palpiform (Fig. 35.16P) or setiform; labial palps separated by less than 2 basal diameters; stipes elongate; frons sometimes with pair of protrusible glands. In leaf litter, moss .....	<b>Pselaphidae</b> (pt, p. 624)
42(36).	Epicranial stem absent; body relatively straight or slightly curved ventrally; head prognathous or slightly declined (Fig. 35.13D); frontal arms absent .....	43
	Epicranial stem moderately long; body strongly curved ventrally (C-shaped) (Figs 35.60B, C); head moderately to strongly hypognathous; frontal arms V-shaped. Case-bearing larvae on leaf surfaces or in leaf litter .....	<b>Chrysomelidae-CRYPTOCEPHALINAE</b> (pt, p. 674)
43(42).	Ratio of antennal length to head width less than 0.15; mandibles distant at base, neither divided nor diverging; mesothoracic leg with 3 or 4 segments; spiracles annular. Ectoparasitic on beetle pupae .....	<b>Carabidae-Lebiini</b> (late instars) (p. 611)
	Ratio of antennal length to head width 0.15 to 0.5; mandibles approximate at base and divided longitudinally, forming 2 pairs of diverging blades or stylets (Fig. 35.16Q); mesothoracic leg with 5 segments, including tarsungulus (Fig. 35.18B); spiracles biforous (Fig. 35.18FF). In rotten wood, leaf litter, under bark .....	<b>Lycidae</b> (pt, p. 638)
44(35).	Epicranial stem and frontal arms absent; mentum or postmentum completely or almost completely connate or fused with maxillae (Figs 35.17N, P, R); hypostomal rods present (Fig. 35.17I) or spiracles annular-biforous (Fig. 35.18EE) or biforous (Fig. 35.18FF) .....	45
	Epicranial stem and frontal arms present; mentum or postmentum completely free or basally connate with maxillae (Fig. 35.17L); hypostomal rods absent; spiracles annular .....	47
45(44).	Ventral mouth-parts strongly protracted (Fig. 35.17I); mandible tridentate; mesal surface of mandibular base with fixed, rigid, acute, hyaline process (Figs 35.16X, Y); spiracles annular. In tunnels of wood-boring beetles, in stored products .....	<b>Cucujidae-PASSANDRINAE</b> (pt, p. 651)
	Ventral mouth-parts retracted; mandibles unidentate; mesal surface of mandibular base simple; spiracles annular-biforous (Fig. 35.18EE) or biforous (Fig. 35.18FF) .....	46
46(45).	Mandibles long and falcate, approximate basally, each divided into 2 parts, so that 4 diverging blades or styli are formed (Fig. 35.16Q); body usually heavily sclerotised, with lateral tergal processes on most segments, and without ventral sclerotised rods on prothorax. In rotten wood, leaf litter, under bark .....	<b>Lycidae</b> (pt, p. 638)
	Mandibles flattened and rounded or subtriangular, not divided; body very lightly sclerotised, with ventral sclerotised rods on prothorax. In rotten wood, in soil associated with roots .....	<b>Throscidae</b> (pt, p. 637)
47(44).	Stemmata absent; antennal sensorium dome-like; labial palps separated by more than 2 basal diameters. In leaf litter .....	<b>Scydmaenidae</b> (pt, p. 621)
	Stemmata on each side 2 or 3; antennal sensorium palpiform (Fig. 35.16P), setiform or sometimes bifid; labial palps	

- separated by less than 2 basal diameters. In leaf litter, moss ..... **Pselaphidae** (pt, p. 624)
- 48(34). T9 without urogomphi ..... 49  
 T9 with urogomphi (Figs 35.18J, N, O) ..... 58
- 49(48). Labial palps 1-segmented ..... 50  
 Labial palps 2-segmented ..... 51  
 Labial palps absent; body minute (length less than 1 mm), fusiform; stemmata on each side 5; head prognathous or slightly declined (Fig. 35.53c); ratio of antennal length to head width more than 0.5; apex of antenna bearing long seta. In flowers, on vegetation, or attached to native bees or wasps ..... **Rhipiphoridae-RHIPIPHORINAE** (triungulins) (p. 663)
- 50(49). Head moderately to strongly hypognathous (Fig. 35.13B); mandibles stylet-like and endognathous; maxillary palp 3-segmented, first segment lacking digitiform appendage; stemmata lacking; setae on tarsungulus 1. Under bark of rotting logs ..... **Cerylonidae** (*Cerylon*) (p. 656)  
 Head prognathous or slightly declined; mandibles well developed, falcate; maxillary palps 4-segmented, the first bearing a digitiform appendage (Fig. 35.17Y); stemmata on each side 6; setae on tarsungulus 4 or more. In ponds and lakes ..... **Hydrophilidae** (*Spercheus*) (p. 617)
- 51(49). T8 without spiracular processes ..... 52  
 T8 with paired processes, each bearing spiracle at apex. On flowers or attached to native bees ..... **Meloidae** (triungulins) (p. 668)
- 52(51). Mandible without groove or perforation ..... 53  
 Mandible with open or partly closed groove; body lightly sclerotised (sometimes with dark pigment pattern), flexible, and clothed with very short, fine pubescence, which gives the surface a dull appearance; paired dorsal glands present on thoracic and most abdominal terga; spiracles small and cribriform or apparently annular. In soil and leaf litter, under stones ..... **Cantharidae** (pt, p. 640)  
 Mandible with internal perforation (Fig. 35.16r); body more heavily sclerotised, with a series of dorsal plates and without fine pubescence or paired dorsal glands (Fig. 35.39i); spiracles well-developed and biforous (Fig. 35.18FF); segment 10 usually with a series of asperate, eversible, anal tubes or holdfast organs (Fig. 35.18cc). In leaf litter ..... **Lampyridae** (p. 640)
- 53(52). Maxillary palps 2-segmented ..... 54  
 Maxillary palps 3-segmented; mala distinct ..... 55  
 Maxillary palps 4-segmented, or if 3-segmented, mala reduced to a brush of hairs ..... 56
- 54(53). Frontal arms absent; head completely visible from above; body elongate; dorsal surfaces very lightly pigmented or sclerotised. In tunnels of ambrosia beetles (Curculionidae: Platypodinae) ..... **Bothrideridae** (*Sosylus* triungulins) (pt, p. 656)  
 Frontal arms present; head not visible from above; body broadly ovate, strongly flattened, and disc-like (Figs 35.49H, J); dorsal surfaces more or less heavily pigmented or sclerotised. In leaf litter, moss ..... **Corylophidae** (pt, p. 658)
- 55(53). Stemmata on each side 3, forming tight cluster or triangle; antennal sensorium short and broad, conical or dome-like; labial palps separated by more than 2 basal diameters; stipes short and broad; thoracic and most abdominal segments with lateral tergal processes. In leaf litter, moss ..... **Scydmaenidae** (pt, p. 621)  
 Stemmata on each side 2 or 3 well-separated and forming row; antennal sensorium more elongate, palpiform (Fig. 35.16p), setiform, or bifid; labial palps separated by less than 2 basal diameters; stipes elongate; thoracic and abdominal segments without lateral tergal processes. In leaf litter, moss ..... **Pselaphidae** (pt, p. 624)
- 56(53). Epicranial stem moderately long; head moderately to strongly hypognathous; body strongly curved ventrally (C-shaped) (Figs 35.60B, C); stemmata on each side 5 or 6. Case-bearing larvae in leaf litter ..... **Chrysomelidae-CRYPTOCEPHALINAE** (pt, p. 674)  
 Epicranial stem absent or very short; head prognathous or slightly declined (Fig. 35.13D); body relatively straight or slightly curved ventrally; stemmata on each side 1 or 0 ..... 57
- 57(56). Paired dorsal glands present on thoracic terga and abdominal terga 1 to 8 or 9; body lightly sclerotised and flexible (sometimes with dark pigment pattern) and clothed with very short, fine pubescence, which gives the surface a dull appearance; spiracles small and cribriform or apparently annular. In soil and leaf litter, under stones ..... **Cantharidae** (pt, p. 640)  
 Paired dorsal glands absent; body usually more heavily sclerotised and rigid, clothed with either setae or occasionally long, fine hairs; spiracles biforous (Fig. 35.18FF). In rotten wood, soil, leaf litter ..... **Elateridae** (pt, p. 637)
- 58(48). Ventral mouth-parts strongly protracted; stipes wider than long; hypostomal rods long and diverging (Fig. 35.17i); mesal surface of mandibular base with 2 to 5 hyaline processes (Fig. 35.16z); 8th spiracles located at ends of long, posteriorly-projecting tubes. In fungus fruiting bodies ..... **Lamingtoniidae** (p. 653)  
 Ventral mouth-parts usually retracted; stipes longer than wide; hypostomal rods absent; mesal surface of mandibular base simple or with a brush of hairs; 8th spiracles laterally placed ..... 59
- 59(58). Epicranial stem absent or very short ..... 60  
 Epicranial stem moderately long ..... 62
- 60(59). Frontal arms absent; cardo absent, indistinct, or membranous; mandibles flattened and more or less triangular; ratio of antennal length to head width less than 0.15. In rotten wood, in soil ..... **Throscidae** (pt, p. 637)  
 Frontal arms present (Fig. 35.16i); cardo distinct and sclerotised (Figs 35.17L, N, R); mandibles narrow and falcate



- (Fig. 35.16s); ratio of antennal length to head width greater than 0.15 ..... 61
- 61(60). Maxillary palps 3-segmented; spiracles annular; mentum, postmentum or labial plate completely free or basally connate with maxillae; ventral epicranial ridges absent; T9 completely dorsal. In leaf litter, moss ..... **Pselaphidae**-Faronini (p. 624)
- Maxillary palps 4-segmented; spiracles biforous (Fig. 35.18FF); mentum, postmentum or labial plate completely or almost completely connate with maxillae (Fig. 35.17N); ventral epicranial ridges present (Fig. 35.17N); T9 extending on to ventral surface (Fig. 35.39L). In rotten wood, soil, leaf litter ..... **Elateridae** (pt, p. 637)
- 62(59). Urogomphi articulated at base (Fig. 35.18J); stemmata on each side 6; ligula present. Under bark, in leaf litter, dung, carrion ..... **Staphylinidae** (pt, p. 621)
- Urogomphi fixed at base; stemmata on each side 3 or less; ligula absent ..... 63
- 63(62). Stemmata absent; labial palps separated by more than 2 basal diameters. In leaf litter ..... **Scydmaenidae** (pt, p. 621)
- Stemmata on each side 2; labial palps separated by less than 2 diameters. In leaf litter, moss ..... **Pselaphidae** (pt, p. 624)
- 64(34). Urogomphi absent; mesothoracic leg with 4 segments or fewer; epicranial stem very short or absent; stemmata absent. In soil ..... **Carabidae**-BRACHININAE (p. 611)
- Urogomphi present and articulated; mesothoracic leg with 5 segments, including tarsungulus; epicranial stem moderately long; stemmata usually present. Under bark, in leaf litter, dung, carrion ..... **Staphylinidae** (pt, p. 621)
- 65(25). Antennae 1-segmented; cardines not distinctly separated from stipites but separated from each other by labium; maxillary palps 2-segmented; labial palps 1-segmented; ventral epicranial ridges absent. In soil, associated with cicada nymphs (ectoparasitic) ..... **Rhipiceridae** (pt, p. 631)
- Antennae 3-segmented; cardines distinctly separated from stipites but closely approximate or contiguous with one another (Fig. 35.17N), not separated by labium; maxillary palps 4-segmented; labial palps 2-segmented; ventral epicranial ridges present (Fig. 35.17N). In soil, leaf litter, rotten wood ..... **Elateridae** (pt, p. 637)
- 66(24). T9 without urogomphi ..... 67
- T9 with urogomphi (Figs 35.18N, Q, S) ..... 70
- 67(66). Abdomen with paired spiracular gills (Figs 35.20B, C); length less than 1.7 mm. In sand, gravel or mud at edges of streams ..... **Microsporidae** (pt, p. 608)
- Thorax and abdomen without spiracular gills. Terrestrial habits ..... 68
- 68(67). Labial palps 1-segmented; maxillary articulating area absent; body slightly to strongly flattened; ventral epicranial ridges absent; prostheca simple ..... 69
- Labial palps 2-segmented; maxillary articulating area present (Figs 35.17K, L, W); body circular in cross-section; ventral epicranial ridges present; prostheca consisting of a brush of comb-hairs (Fig. 35.17B). Under bark, in rotten wood, or associated with ascomycete fungi ..... **Biphyllidae** (pt, p. 654)
- 69(68). Body broadly ovate, strongly flattened and disc-like (Figs 35.49H, J); stemmata on each side 2; ratio of antennal length to head width more than 0.5; spiracles annular; cardines indistinct or absent. In leaf litter ..... **Corylophidae** (pt, p. 658)
- Body not broadly ovate and strongly flattened; stemmata on each side 3 or 4; ratio of antennal length to head width less than 0.5; spiracles annular-biforous (Fig. 35.18EE) or biforous (Fig. 35.18FF); cardines distinct, more or less elongate. On plant surfaces (feeding on coccids) ..... **Nitidulidae**-CYBOCEPHALINAE (p. 649)
- 70(66). Abdominal spiracles annular ..... 71
- Abdominal spiracles annular-biforous (Fig. 35.18EE); body elongate and strongly flattened with dorsal and ventral rows of abdominal asperities forming incomplete circles (Fig. 35.18E); urogomphi well developed. Under bark ..... **Phloeostichidae**-HYMAEINAE (p. 650)
- Abdominal spiracles cribriform (Fig. 35.18HH); body elongate, convex, and more or less curved ventrally; urogomphi minute; antennae 2-segmented (or 3-segmented with a very small terminal segment); setae on tarsungulus 4 or more; epipharynx and hypopharynx with a complex series of sclerotised plates and combs. In soil, under rocks ..... **Dascillidae** (p. 631)
- 71(70). Ratio of antennal length to head width less than 0.15; antennal sensorium on segment 1, not on segment 2; ventral mouth-parts strongly protracted (Fig. 35.17I); stipes wider than long; epicranial stem absent; abdominal segment 10 absent or completely concealed (Fig. 35.18V). On plant surfaces affected by rusts or smuts ..... **Phalacridae** (pt, p. 653)
- Ratio of antennal length to head width more than 0.5; antennal sensorium on segment 2; ventral mouth-parts retracted; stipes longer than wide; epicranial stem present; abdominal segment 10 distinct and visible from above (Fig. 35.18Q). Under bark ..... **Silvanidae**-ULEIOTINAE (pt, p. 651)
- 72(22). T8 without special armature ..... 73
- T8 with single median process, simple at apex; T9 with paired, articulated urogomphi; coxal bases and S1 to S3 with ventral gill tufts. In ponds or lakes ..... **Hygrobiidae** (p. 614)
- T8 with single median process bearing spiracles at apex (Figs 35.18R, 22G); articulated urogomphi usually present. In a variety of aquatic environments ..... **Dytiscidae** (p. 616)
- 73(72). T9 without urogomphi, or forming with T8 a large, concave disc ..... 74
- T9 with urogomphi (Figs 35.13D, 18R) ..... 80
- 74(73). Mandible with internal perforation (Fig. 35.16T); dorsal surfaces granulate-spinose or abdominal segments with lateral gills. Aquatic ..... 75

- Mandible without internal perforation, sometimes with open or partly closed groove (Fig. 35.16s); dorsal surfaces not granulate or spinose, sometimes with rows or patches of asperities; abdominal segments without lateral gills. Terrestrial ..... 76
- 75(74). Mandibles narrow and falcate (Fig. 35.16t); ratio of antennal length to head width more than 0.5; maxillary palps 4-segmented; labial palps 3-segmented; dorsal surfaces smooth; abdominal segment 10 with 2 pairs of hooks; abdominal segments 1 to 8 each with pair of lateral gills, segment 9 with 2 pairs (Fig. 35.22j). In ponds or pools ..... **Gyrinidae** (p. 616)
- Mandibles broad at base and narrow at apex; ratio of antennal length to head width less than 0.5; maxillary palps 3-segmented; labial palps 2-segmented; dorsal surfaces granulate or spinose; abdominal segment 10 without 2 pairs of hooks; abdominal segments without lateral gills. In ponds ..... **Haliplidae** (p. 614)
- 76(74). T8 and T9 forming a large, concave disc, sometimes bearing branched processes ..... **Carabidae-PAUSSINAE** (p. 611)
- T9 simple, not forming concave disc ..... 77
- 77(76). Apex of maxilla without distinct lobes, its surface and that of labium sometimes covered with fine fringed membranes; labial palps 1-segmented; abdominal terga 1 to 7 or 8 each with 2 rows of asperities, which may form incomplete rings. In rotten wood ..... **Rhysodidae** (p. 609)
- Apex of maxilla with 1 or 2 distinct lobes (Figs 35.17j, u), without fringed membranes; labial palps 2-segmented ..... 78
- 78(77). T5 to T7 each with transverse row of 4 spines (Fig. 35.21j); maxilla with separate galea and lacinia (Fig. 35.17u). In burrows around ant nests ..... **Carabidae-PSEUDOMORPHINAE** (pt, p. 611)
- T5 with distinct protuberance bearing 2 or 3 pairs of hooks (Fig. 35.21k); maxilla with single mala. In burrows in soil ..... **Carabidae-CICINDELINAE** (p. 611)
- Abdominal terga without hooks or spines ..... 79
- 79(78). Frontal arms distinctly separated at base (Fig. 35.16i); stemmata absent; abdomen pale and white, somewhat physogastric. In ant nests ..... **Carabidae-PSEUDOMORPHINAE** (pt, p. 611)
- Frontal arms contiguous (Fig. 35.13d); stemmata present; abdomen moderately to heavily sclerotised, not physogastric ..... **Carabidae** (pt, p. 611)
- 80(73). Abdominal segment 10 distinct and visible from above (Fig. 35.13d); S9 exposed; gular sutures fused (Fig. 35.17j); ligula almost always present. Usually terrestrial ..... **Carabidae** (pt, p. 611)
- Abdominal segment 10 absent or completely concealed; S9 concealed; gular sutures separate (Fig. 35.17k); ligula absent. In lakes or ponds ..... **Noteridae** (p. 615)
- 81(3). T9 without paired processes or urogomphi ..... 82
- T9 with pair of urogomphi (Figs 35.18n, o, q-bb) ..... 135
- 82(81). Antennae 1-segmented ..... 83
- Antennae 2-segmented ..... 89
- Antennae 3-segmented ..... 101
- 83(82). Mesothoracic leg with 1 or 2 segments ..... 84
- Mesothoracic leg with 3 or 4 segments (Fig. 35.18d); T9 with median sclerotised process (Fig. 35.52a). In rotten wood, stems or fungus fruiting bodies ..... **Mordellidae** (pt, p. 663)
- Mesothoracic leg with 5 segments, including tarsungulus (Fig. 35.18b) ..... 86
- 84(83). Labrum with tormae extending from posterolateral angles, but without unattached labral rods; mandibular mola (Fig. 35.17f) and hypopharyngeal sclerome (Fig. 35.17z) present. In dead wood, stems, vines, fungus fruiting bodies ..... **Anthribidae** (pt, p. 679)
- Labral rods present (Fig. 35.16n); mandibular mola and hypopharyngeal sclerome absent ..... 85
- 85(84). Median endocarina coincident with epicranial stem (Fig. 35.16j); stemmata absent; patch of asperities present on each side of mesotergum; legs longer than wide, not lobe-like. In dead wood, under bark ..... **Brentidae-BRENTINAE** (p. 680)
- Median endocarina extending anterad of epicranial stem (Fig. 35.16l); 1 pair of stemmata present; patches of mesotergal asperities absent; legs shorter than wide, rounded and lobe-like. In tubers of Convolvulaceae, especially sweet potato (*Cylas*) or in stems of aquatic plants (*Nanophyes*) ..... **Brentidae-CYLADINAE, NANOPHYINAE** (p. 680)
- 86(83). Maxilla with single mala (Figs 35.17q, s); abdominal segment 10 without oval lobes separated by longitudinal groove; frontal arms present (Figs 35.16l, k-m) ..... 87
- Maxilla with separate galea and lacinia (Fig. 35.17v); abdominal segment 10 with pair of oval lobes separated by longitudinal groove (Fig. 35.18m); frontal arms absent ..... 88
- 87(86). Maxillary palps 2-segmented; body oblong to ovate; median endocarina absent; apex of mandible bidentate (Fig. 35.17g); stemmata on each side 3; spiracles annular; legs not reduced; ligula not sclerotised. On plant surfaces ..... **Coccinellidae** (pt, p. 658)
- Maxillary palps 3-segmented; body elongate and more or less parallel-sided; median endocarina extending anterad of epicranial stem (Fig. 35.16l); apex of mandible with 3 or more teeth in row (Fig. 35.16aa); stemmata on each side 2 or less; spiracles annular; legs not reduced; ligula not sclerotised. In leaf litter, soil, on plant surfaces ..... **Chrysomelidae-GALERUCINAE** (pt, p. 674)
- Maxillary palps 4-segmented; body elongate and cylindrical, heavily sclerotised; median endocarina absent; apex of mandible tridentate (Fig. 35.16y); stemmata on each side 0; spiracles biforous (Fig. 35.18ff); legs reduced; ligula



- forming sclerotised, 4-dentate, wedge-like plate (Fig. 35.17s); abdominal apex with dorsally-hinged operculum (Fig. 35.18k). In rotten wood ..... **Callirhipidae** (pt, p. 635)
- 88(86). Thoracic spiracle located at anterior end of prothorax; abdominal terga without bands of asperities. In dung, animal nests, stored products ..... **Anobiidae-PTININAE** (p. 643)
- Thoracic spiracle located at posterior end of prothorax; abdominal terga usually with bands of asperities. In dead wood, twigs, fungus fruiting bodies, stored products ..... **Anobiidae** (pt, p. 643)
- 89(82). Labial palps absent (or represented by minute papillae only); head strongly retracted (Fig. 35.16a) ..... 90
- Labial palps well developed ..... 91
- 90(89). Body strongly curved ventrally (C-shaped) (Fig. 35.42i); legs moderately well developed and prothorax never greatly enlarged and flattened; spiracles annular-biforous. In seeds or pods of various plants ..... **Chrysomelidae-BRUCHINAE** (pt, p. 674)
- Body straight or sometimes curved laterally; prothorax greatly enlarged and flattened (Fig. 35.39a); legs minute, with 1 or 2 segments; spiracles cribriform (Fig. 35.18hh). Under bark or in wood ..... **Buprestidae** (pt, p. 632)
- 91(89). Labial palps 1-segmented ..... 92
- Labial palps 2-segmented ..... 94
- 92(91). Head deeply emarginate posteriorly and more or less retracted into thorax; 8th abdominal spiracles terminal, placed on a pair of posteriorly-projecting, spine-like processes; body more or less flattened and parallel sided. Leaf-miners ..... **Chrysomelidae-HISPINAE** (pt, p. 674)
- Head protracted and not deeply emarginate posteriorly; 8th abdominal spiracles not terminal, not on spine-like processes; body not flattened and parallel sided ..... 93
- 93(92). Head prognathous or slightly declined (Fig. 35.13d); stemmata on each side 1; body elongate, without narrow processes. In soil, leaf litter, on leaf surfaces ..... **Chrysomelidae-GALERUCINAE** (pt, p. 674)
- Head moderately to strongly hypognathous (Fig. 35.13b); stemmata on each side 5 or 6; body either ovate with a number of long, narrow, lateral processes (Fig. 35.60e) or more elongate with a single long, narrow process at abdominal apex. On leaf surfaces or in leaf axils ..... **Chrysomelidae-HISPINAE** (pt, p. 674)
- 94(91). Median endocarina absent or coincident with epicranial stem (Fig. 35.16j) ..... 95
- Median endocarina extending anterad of epicranial stem (Figs 35.16h, l), or if epicranial stem absent, then endocarina beginning at middle of head and not extending to base ..... 99
- 95(94). Body relatively straight or slightly curved ventrally; T3 without transverse folds; abdominal segment 10 without oval lobes separated by longitudinal groove ..... 96
- Body strongly curved ventrally (C-shaped) (Fig. 35.42i); T3 with 2 or more transverse plicae; abdominal segment 10 with pair of oval lobes separated by longitudinal groove (Fig. 35.18m). In dead wood, twigs, fungus fruiting bodies, stored products ..... **Anobiidae** (pt, p. 643)
- 96(95). T9 without median process (entire tergum may form spine) ..... 97
- T9 with median process (Fig. 35.52a); body more or less cylindrical and lightly sclerotised; head moderately to strongly hypognathous; stemmata absent. In rotten wood, stems, fungus fruiting bodies ..... **Mordellidae** (pt, p. 663)
- 97(96). Body not broadly ovate and strongly flattened; cardines if present, separated from each other by labium; ratio of antennal length to head width less than 0.15; abdominal segment 10 exposed; T9 not forming spine ..... 98
- Body broadly ovate, strongly flattened, and disc-like (Fig. 35.39h); cardines completely fused forming single plate; ratio of antennal length to head width more than 0.5; abdominal segment 10 concealed; T9 forming articulated spine. Under bark or stones in dry areas ..... **Brachypsectridae** (pt, p. 636)
- 98(97). Gula absent; body elongate and more or less cylindrical, lightly sclerotised; head moderately to strongly hypognathous (Fig. 35.52a); stemmata absent. In rotten wood, stems, fungus fruiting bodies ..... **Mordellidae** (pt, p. 663)
- Gula wider than long; body more oblong or ovate and somewhat flattened; dorsal surfaces of abdominal segments usually with transverse row of 6 protuberances, which may bear setose or branched processes (Fig. 35.18f); head prognathous or slightly declined (Fig. 35.50k); stemmata on each side 3. On plant surfaces ..... **Coccinellidae** (pt, p. 658)
- Gula longer than wide; body elongate, with enlarged abdomen (physogastric), lightly sclerotised; head prognathous or slightly declined; stemmata on each side 0 or 1. In tunnels of wood-boring beetles ..... **Bothrideridae-BOTHRIDERINAE** (pt, p. 656)
- 99(94). Head strongly retracted (Fig. 35.16a); gular region present (separating labium from thorax); legs reduced and often with fewer than 5 segments. Under bark, in living or dead wood ..... **Cerambycidae** (pt, p. 672)
- Head protracted or slightly retracted (Fig. 35.13d); gular region absent (labium contiguous with thoracic membrane); legs well developed. On leaf surfaces, in leaf litter or soil ..... 100
- 100(99). Maxillary palps 2-segmented; ratio of length of abdomen to length of thorax 1.2 to 2; T8 with paired processes or a forked process (Fig. 35.60e). On leaf surfaces ..... **Chrysomelidae-HISPINAE** (pt, p. 674)
- Maxillary palps 3-segmented; ratio of length of abdomen to length of thorax more than 2; T8 without special armature. In leaf litter, soil, on plant surfaces ..... **Chrysomelidae-GALERUCINAE** (pt, p. 674)
- 101(82). Abdominal apex without hinged operculum ..... 102
- Abdominal apex with ventrally hinged operculum (Fig. 35.18i) ..... 131
- 102(101). Median endocarina absent or coincident with epicranial stem (Fig. 35.16j) ..... 103

- Median endocarina Y-shaped, coincident with epicranial stem and frontal arms ..... **Melandryidae** (pt, p. 662)
- Median endocarina extending anterad of epicranial stem (Fig. 35.16L), or if epicranial stem absent, then endocarina beginning at middle of head and not extending to base ..... 124
- Median endocarina located between frontal arms (Fig. 35.16K); epicranial stem absent, endocarina beginning at base of head ..... 130
- 103(102). Maxilla without apical lobes; body very lightly sclerotised; stemmata on each side 1. In cells of native bees ..... **Meloidae** (pt, p. 668)
- Maxilla with single mala (Figs 35.17K–M, Q) ..... 104
- Maxilla with separate galea and lacinia (Figs 35.17R, T, V) ..... 118
- 104(103). Labial palps 1-segmented ..... 105
- Labial palps 2-segmented ..... 106
- Labial palps absent; body strongly curved ventrally (C-shaped) (Fig. 35.13C) and lightly sclerotised; head strongly retracted (Fig. 35.16A). In seeds or pods of various plants ..... **Chrysomelidae-BRUCHINAE** (pt, p. 674)
- 105(104). Epicranial stem absent or very short; stipes longer than wide; gular region present (separating labium from thorax) (Figs 35.17K–M); mesal surface of mandibular base with fixed, rigid, hyaline process, sometimes partly sclerotised (Fig. 35.16X); apex of mandible with single tooth; stemmata on each side 3. On plant surfaces ..... **Coccinellidae** (pt, p. 658)
- Epicranial stem moderately long; stipes wider than long; gular region absent (labium contiguous with thoracic membrane) (Fig. 35.17Q); mesal surface of mandibular base simple or slightly expanded; apex of mandible with 4 or more teeth in row (Fig. 35.16AA); stemmata on each side 6; body often covered in slime. On plant surfaces ..... **Chrysomelidae-CRIOCERINAE** (p. 674)
- 106(104). Body relatively straight or slightly curved ventrally; head protracted or slightly retracted ..... 107
- Body strongly curved ventrally (C-shaped) (Figs 35.13B, C); head strongly retracted (Fig. 35.16A); gular region absent (labium contiguous with thoracic membrane) (Fig. 35.17Q). In soil among roots; in egg cases on vegetation ..... **Chrysomelidae-SAGRINAE** (pt, p. 674)
- 107(106). Mouth-parts not forming sucking tube; head not concealed from above by prothorax ..... 108
- Mouth-parts forming sucking tube; head completely concealed from above by prothorax. In leaf litter, rotten wood, fungi ..... **Cerylonidae-CERYLONINAE** (p. 656)
- 108(107). T9 without median process (entire tergum may form spine) ..... 109
- T9 with median process (Fig. 35.52A). In rotten wood, stems, fungus fruiting bodies ..... **Mordellidae** (pt, p. 663)
- 109(108). Head prognathous or slightly declined (Fig. 35.13D) ..... 110
- Head moderately to strongly hypognathous (Fig. 35.13B) ..... 117
- 110(109). Body not broadly ovate and strongly flattened; cardines if present, separated from each other by labium; visible abdominal segments 10; T9 not forming articulated spine ..... 111
- Body broadly ovate, strongly flattened, and disc-like (Fig. 35.39H); cardines completely fused forming single plate; visible abdominal segments 9; T9 forming articulated spine; thoracic segments and abdominal segments 1–8 each with pair of lateral, branched processes; body covered with scale-like setae; mandibles internally perforated (Fig. 35.16T). Under bark or stones in dry areas ..... **Brachyssectridae** (pt, p. 636)
- 111(110). Stipes longer than wide ..... 112
- Stipes wider than long ..... 116
- 112(111). Epicranial stem absent ..... 113
- Epicranial stem present (Figs 35.16J, L) ..... 114
- 113(112). Hypostomal rods absent; frontal arms absent; setae on tarsungulus 0; stemmata on each side 1; dorsal surfaces of abdominal segments without transverse row of protuberances. In cells of native bees ..... **Meloidae** (pt, p. 668)
- Hypostomal rods present; frontal arms present; setae on tarsungulus 1; stemmata on each side 3; dorsal surfaces of abdominal segments with transverse row of 6 protuberances, which may bear branched or setose processes (Fig. 35.18F). On plant surfaces ..... **Coccinellidae** (pt, p. 658)
- 114(112). Frontoclypeal suture absent or vaguely indicated; hypostomal rods absent; abdominal segment 10 distinct and visible from above (Fig. 35.27D); apex of mandible not multidentate; dorsal surfaces of abdominal segments without transverse row of protuberances; apex of antennal segment 2 oblique, so that sensorium arises proximad of segment 3 (Fig. 35.16P). Usually under bark, in leaf litter or in rotten wood ..... **Staphylinidae** (pt, p. 621)
- Frontoclypeal suture distinct (Figs 35.16J, L); hypostomal rods present or mandibular apex multidentate; apex of antennal segment 2 truncate, so that sensorium and segment 3 arise together (Fig. 35.16O) ..... 115
- 115(114). Hypostomal rods present, usually long and diverging posteriorly; body elongate and more or less parallel sided, lightly sclerotised, sometimes with paired dorsal and ventral protuberances (ampullae); apex of mandible bidentate; stemmata on each side 5 or 0. In rotten wood, fungus fruiting bodies ..... **Melandryidae** (pt, p. 662)
- Hypostomal rods absent; body oblong or ovate; dorsal surfaces of abdominal segments each with transverse row of 6 protuberances, which bear branched processes (Fig. 35.18F); apex of mandible multidentate; stemmata on each side 3. On plant surfaces ..... **Coccinellidae-EPIACHNINAE** (p. 658)
- 116(111). Ventral mouth-parts strongly protracted (Figs 35.17I, J); gula much longer than wide; apex of antennal segment 2 truncate, so that sensorium and segment 3 arise close together (Fig. 35.16O); spiracles annular-biforous; T9 with a sclerotised plate. In fungus fruiting bodies, stored products ..... **Cleridae-THANEROCLERINAE** (p. 645)
- Ventral mouth-parts retracted; gula not or only slightly longer than wide; apex of antennal segment 2 oblique, so



that sensorium arises proximad of segment 3 (Fig. 35.16p); spiracles annular; T9 without sclerotised plate. In leaf litter, rotten wood, carrion, dung, under bark ..... **Staphylinidae** (pt, p. 621)

- 117(109). Gula absent (Fig. 35.17q); mandible broad and stout or more or less wedge-like, with a single lobe or tooth at apex (Fig. 35.16cc); body elongate and cylindrical, lightly sclerotised. In rotten wood, stems, fungus fruiting bodies ..... **Mordellidae** (pt, p. 663)

Gula present (Fig. 35.17k); mandible with 2 or more teeth at apex; body more oblong or ovate and slightly flattened, often with transverse rows of dorsal protuberances. Under loose bark, on surfaces of vegetation ..... **Coccinellidae** (pt, p. 658)

- 118(103). Maxillary articulating area well developed but concealed behind lateral edges of expanded postmentum, which is divided longitudinally into 3 parts (Fig. 35.39j); anal hooks 3 or more on each side (Fig. 35.39f); gular sutures separate; mesal surface of mandibular base with brush of hairs. In plant debris in or near streams ..... **Ptilodactylidae-ANCHYTARSINAE** (p. 635)

Postmentum not divided longitudinally into 3 parts; if maxillary articulating area concealed behind expanded postmentum, gular sutures are fused (Figs 35.17j, p) and mesal surface of mandibular base with articulated process (Fig. 35.16v) ..... 119

- 119(118). Body broadly ovate, strongly flattened and disc-like (Fig. 35.39h); T9 forming articulated spine; mandibles narrow and falcate, with internal perforation (Fig. 35.16r). Under bark or stones in dry areas ..... **Brachypsectridae** (pt, p. 636)

Body not broadly ovate and strongly flattened ..... 120

- 120(119). Anterior abdominal spiracles absent or non-functional; spiracles on segment 8 forming pair of projecting spines (Fig. 35.18h); body strongly curved ventrally (C-shaped) (Figs 35.13b, c) and lightly sclerotised; head protracted or slightly retracted. On roots and stems of aquatic plants ..... **Chrysomelidae-DONACIINAE** (p. 674)

All abdominal spiracles annular or annular-uniformous (Fig. 35.18dd), those on segment 8 not forming pair of spines ..... 121

All abdominal spiracles annular-biforous (Fig. 35.18ee) or biforous (Fig. 35.18ff), those on segment 8 not forming pair of spines ..... 122

- 121(120). Body strongly curved ventrally (C-shaped) (Fig. 35.42j); head strongly retracted (Fig. 35.16a); T3 with 2 or more transverse plicae; abdominal segment 10 with pair of oval lobes separated by longitudinal groove (Fig. 35.18m); vestiture consisting of fine hairs or setae only. In dead wood ..... **Bostrichidae** (pt, p. 642)

Body relatively straight or only slightly curved ventrally; head protracted or slightly retracted; T3 without transverse plicae; segment 10 without oval lobes; vestiture including specialised setae (barbed spicisetae (Fig. 35.16e) or complex hastisetae (Fig. 35.16f)). On a variety of animal and plant products ..... **Dermestidae** (pt, p. 642)

- 122(120). Epicranial stem very short or absent (Figs 35.16k, m); stemmata on each side 1 or 5–6 forming tight cluster; abdominal apex with 3 or more anal hooks on each side (Fig. 35.39f); gular sutures fused (Fig. 35.17p). In leaf litter, flood debris ..... **Ptilodactylidae-PTILODACTYLINAE** (p. 635)

Epicranial stem moderately long (Fig. 35.16l); stemmata on each side 5 or 6, well separated and not forming tight cluster; without anal hooks or with only one on each side; gular sutures separate ..... 123

- 123(122). Maxillary articulating area absent (Fig. 35.17r); cardines contiguous, not separated by labium; setae on tarsungulus 1; mesal surface of mandibular base simple. In leaf litter, soil, flood debris ..... **Limnichidae** (p. 634)

Maxillary articulating area present (Fig. 35.17k); cardines separated from each other by labium; setae on tarsungulus 2; mesal surface of mandibular base with brush of hairs (Fig. 35.16r). In mosses, liverworts, soil, among roots ..... **Byrrhidae** (p. 634)

- 124(102). Mesothoracic leg with fewer than 5 segments; head strongly retracted (Fig. 35.16a); body lightly sclerotised. Under bark, in living and dead wood ..... **Cerambycidae** (pt, p. 672)

Mesothoracic leg with 5 segments, including tarsungulus (Fig. 35.18b) ..... 125

- 125(124). Head protracted or slightly retracted (Figs 35.13a–d) ..... 126

Head strongly retracted (Fig. 35.16a) ..... 129

- 126(125). Maxillary mala cleft at apex (Fig. 35.17x); mesal surface of mandibular base with membranous, setose lobe (Fig. 35.16ee); apex of T9 with median, spine-like process (Fig. 35.50g). In fungus fruiting bodies ..... **Erotylidae (Microsternus)** (p. 654)

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- 164(161). S9 completely concealed beneath S8 (Fig. 35.18V); hypostomal rods long and diverging (Fig. 35.17I); apex of mandible tridentate; mesal surface of mandibular base with 1 or more hyaline processes (Fig. 35.16Z); 8th abdominal spiracles located at posterior end of segment and facing posteriorly. In flower heads, rotting wood, fungus fruiting bodies ..... **Phalacridae** (pt, p. 653)
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- 168(167). Epicranial stem very short; ratio of antennal length to head width 0.15 to 0.5; frontal arms lyriform (Figs 35.16I, K); molar surface with numerous fine ridges (Fig. 35.17H); ligula present (Fig. 35.17K); body relatively straight or slightly curved ventrally and heavily pigmented dorsally. On bark and rock surfaces covered with algae, moss and lichens ..... **Tenebrionidae**-Leiochrini (p. 665)
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- 171(170). Metathoracic leg reduced and 1-segmented (Fig. 35.29D); maxilla with galea and lacinia; spiracles cribriform (Fig. 35.18HH). In rotten wood ..... **Passalidae** (p. 627)  
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- 178(177). Head moderately to strongly hypognathous (Fig. 35.43C), globular; prothorax enlarged and swollen dorsally (hump-like); body very elongate, with abdomen more than 5 times as long as thorax; patches of asperities on lateral portions of all thoracic segments and on apex of T9, which is blunt and rounded (Fig. 35.43D). In rotten wood ..... **Lymexylidae** (pt, p. 644)  
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- 185(177). Stemmata on each side 5; stemmata large, each with well-developed lens; maxillary palps 3-segmented; head prognathous or slightly declined (Fig. 35.13D); ratio of antennal length to head width less than 0.15; body relatively straight or slightly curved ventrally, heavily pigmented dorsally; ventral epicranial ridges present (Fig. 35.17N); labium almost completely connate with maxillae (Fig. 35.17R). In sand or mud along streams ..... **Heteroceridae** (pt, p. 634)
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- 187(186). T3 with 3 distinct transverse plicae, each bearing one or more rows of short, stiff setae; meso- and metathoracic legs not forming stridulatory organs; head much more darkly pigmented than body (except for prothoracic shield). In carcasses ..... **Trogidae** (p. 627)
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- 188(175). Abdominal terga without rows of asperities; ratio of antennal length to head width 0.15 to 0.5; head prognathous or slightly declined (Fig. 35.13D); ventral epicranial ridges absent; thoracic terga without patches of asperities ..... 189
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- 189(188). Frontal arms lyriform (Figs 35.16K, M); posterior edge of head capsule distinctly emarginate dorsally; process on T9 lightly pigmented, rounded and deciduous (Fig. 35.18P) OR hypostomal rods present (Fig. 35.17L), frontoclypeal suture absent, and spiracles annular-biforous (Fig. 35.18EE) ..... 190
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- 190(189). Paired endocarinae absent; frontoclypeal suture distinct; apex of mala cleft (Fig. 35.17x); hypostomal rods absent; abdominal spiracles annular; median process on T9 lightly sclerotised, rounded apically, pubescent and deciduous (Fig. 35.18P). In leaf litter ..... **Scaptiidae** (p. 671)
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- 192(174). T9 forming articulated plate bearing median, forked process (Fig. 35.50D); abdominal S9 almost completely concealed by S8 (Fig. 35.18v); body elongate, more or less parallel sided and strongly flattened. Under bark ..... **Cucujidae**-CUCUJINAE (p. 651)
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- concave, not tuberculate or asperate; segment 10 with single, long pygopod; spiracles cribriform (Figs 2.11B; 35.18GG); body clothed with dark, stiff hairs. In sand and mud along streams ..... **Heteroceridae** (pt, p. 634)
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- 205(174). T8 without special armature; bases of frontal arms contiguous (Fig. 35.16M); head moderately to strongly hypognathous (Fig. 35.13B); frontoclypeal suture absent or vaguely indicated; hypostomal rods present (Figs 35.17I, L); stemmata on each side 4 or fewer. Under bark, in fungus fruiting bodies, on bark surfaces ..... **Endomychidae** (pt, p. 657)
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- 229(227). Apex of mala cleft (Fig. 35.17x); hypostomal rods short and diverging posteriorly; T9 distinctly tuberculate; urogomphi without pit between them; ligula as long as or longer than labial palps. Under bark, in fungus fruiting bodies ..... **Zopheridae (Meryx)** (p. 664)  
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- Hypostomal rods present ..... 234
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- 234(231). Epicranial stem long and bent to the left; frontal arms joined anteriorly by transverse ecdysial line; spiracles on segment 8 much larger than those on 7. In fungus fruiting bodies. Known from New Guinea ..... **Pterogeniidae**
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- 237(211). Urogomphi articulated at base (Fig. 35.18r); maxilla with fixed galea and lacinia, sometimes fused or connate for part of their lengths; galea often with fringe of setae at apex (fimbriate galea) (Fig. 35.17T) ..... 238
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- 240(238). Stemmata present; epicranial suture present; vestiture often including expanded setae (Fig. 35.16D). In leaf litter, fungi, carrion ..... **Leiodidae** (pt, p. 619)
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- Mala falcate and not cleft at apex (Fig. 35.17W); head prognathous or slightly declined (Fig. 35.13D); hypostomal rods usually long ..... 248
- 248(247). Ventral epicranial ridges present (Fig. 35.17N); frontal arms separated at base (Fig. 35.16I); tarsungulus with 2 subequal setae lying side by side. In rotting vegetation, cycad cones, leaf axils ..... **Languriidae-XENOSCELINAE** (p. 654)
- Ventral epicranial ridges absent; frontal arms contiguous at base (Fig. 35.16K); tarsungulus with 2 unequal setae lying one distal to the other, or occasionally with 1 seta only. In leaf litter, decaying vegetation ..... **Languriidae-CRYPTOPHILINAE** (p. 654)
- 249(245). Mala truncate (Figs 35.17K, X) or rounded (Figs 35.17L, M) ..... 250
- Mala falcate (Fig. 35.17W) ..... 252
- 250(249). Ratio of antennal length to head width less than 0.15; stemmata on each side 2. On moulds, in stored products ..... **Endomychidae (Mycetaea)** (p. 657)
- Ratio of antennal length to head width more than 0.15; stemmata on each side 5 or 6 ..... 251
- 251(250). Labial palps 1-segmented; hypostomal rods long and diverging posteriorly; dorsal surfaces with numerous elongate, setiferous tubercles. In rotting fungus fruiting bodies ..... **Hobartiidae** (pt, p. 653)
- Labial palps 2-segmented; hypostomal rods very short; dorsal surfaces granulate-tuberculate, but without elongate, setiferous tubercles. In fruiting bodies of higher fungi ..... **Erotylidae-DACNINAE** (pt, p. 654)
- 252(249). Labial palps 1-segmented ..... 253
- Labial palps 2-segmented ..... 255
- 253(252). Hypostomal rods absent; ventral epicranial ridges present (Fig. 35.17N); dorsal surfaces granulate or tuberculate; urogomphi not strongly upturned. In leaf litter, decaying vegetation, under bark, on spore-covered fungal surfaces ..... **Rhizophagidae-MONOTOMINAE** (p. 650)
- Hypostomal rods long and diverging posteriorly; ventral epicranial ridges absent; dorsal surfaces smooth or with elongate, setiferous tubercles; urogomphi strongly upturned (Fig. 35.18N) ..... 254
- 254(253). Dorsal surfaces smooth, without setiferous tubercles; spiracles not placed at the ends of tubes. In leaf litter, rotten wood, fungi, bee nests, stored products ..... **Cryptophagidae-CRYPTOPHAGINAE** (p. 653)
- Dorsal surfaces covered with elongate, setiferous tubercles; spiracles placed at the ends of short tubes (Fig. 35.18S). In rotting fungus fruiting bodies ..... **Hobartiidae** (pt, p. 653)
- 255(252). Thoracic and abdominal segments bearing lateral tergal processes; body more or less ovate ..... 256
- Thoracic and abdominal segments without lateral tergal processes; body elongate and more or less parallel sided ..... 257
- 256(255). Abdominal spiracles located at ends of tergal processes; dorsal surfaces more or less granulate (often covered with dirt); stemmata on each side 5; accessory ventral process of mandible present (Figs 35.17B–E). In leaf litter ..... **Phloeostichidae-PRIASILPHINAE** (p. 650)
- Abdominal spiracles not located at ends of tergal processes; dorsal surfaces not granulate; stemmata on each side 1 or 0; accessory ventral process of mandible absent. In fungi, rotten wood, leaf litter ..... **Endomychidae-MYCHOTHENINAE** (pt, p. 657)
- 257(255). T9 (not including urogomphi) much shorter than T8 (Fig. 35.18Q); segment 10 posteriorly oriented; body more or less flattened; urogomphi approximate and more or less parallel. In leaf litter and stored products ..... **Silvanidae-ULEIOTINAE** (pt, p. 651)
- T9 well developed, about as long (not including urogomphi) as T8; segment 10 posteroventrally oriented; body not or only slightly flattened ..... 258
- 258(257). Urogomphi accompanied by a series of 12 elongate, flattened tubercles distributed around the periphery of T9; anterior abdominal terga bearing a number of shorter, flattened tubercles; spiracles placed at the ends of spiracular tubes. In tree fern crowns ..... **Protocucujidae** (p. 649)
- T9 simple, except for pair of short urogomphi; dorsal surfaces smooth; spiracles not placed at the ends of tubes ..... 259
- 259(258). Stemmata on each side 6; mala articulated at base; segment 10 with 2 long, tubular pygopods. In male cones of cycads ..... **Boganiidae-PARACUCUJINAE** (p. 650)
- Stemmata on each side 1 or 0; mala fixed at base; segment 10 without long, tubular pygopods. In leaf litter, grass piles, stored products ..... **Cryptophagidae-ATOMARIINAE** (pt, p. 653)
- 260(211). Head strongly retracted (Fig. 35.16A); body strongly curved ventrally (C-shaped) (Fig. 35.42J); 8th abdominal spiracle much larger than others. In dead wood ..... **Bostrichidae-LYCTINAE** (1st instar) (p. 642)
- Head protracted or slightly retracted; body not strongly curved ventrally; 8th abdominal spiracle about the same size as others. In fungus fruiting bodies ..... **Erotylidae** (pt, p. 654)
- 261(210). Each urogomphus with 1 or 2 small, mesal teeth near base; hypostomal rods short; paired endocarinae absent; mola well developed and tuberculate or asperate (Figs 35.17C–E) ..... 262
- Urogomphi bifurcate (Figs 35.18S, Z, AA); hypostomal rods extending almost to posterior edge of head (Fig. 35.17L); paired endocarinae coincident with frontal arms (Fig. 35.16M); mola consisting of a few teeth only.

- Under bark, in rotten wood, stems, leaf litter ..... **Salpingidae**-SALPINGINAE (pt, p. 669)
- 262(261). Stemmata 5 on each side; mala cleft at apex; urogomphi each with 2 teeth at base. In sand or under litter on beaches ..... **Anthicidae** (*Lagrioida*) (p. 671)
- Stemmata absent; mala not cleft; urogomphi each with a single tooth at base. In rotting vegetation ..... **Salpingidae** (*Aglenus*) (p. 669)
- 263(210). Stemmata on each side 1; ligula well developed and labial palps distinctly separated (Fig. 35.17K). Under bark ..... **Salpingidae**-PROSTOMINIINAE (pt, p. 669)
- Stemmata on each side 2 or 5; ligula absent and labial palps subcontiguous (Fig. 35.17L). Under bark ..... **Salpingidae**-INOPEPLINAE (p. 669)
- 264(210). Row of basal asperities on S9 straight or slightly sinuate (Fig. 35.18X) ..... 265
- Row of basal asperities on S9 strongly, doubly curved; T9 bearing complex urogomphi with single pit between them and 6–8 tubercles forming row in front of them. Under bark, in rotten wood ..... **Pythidae**-PYTHINAE (p. 668)
- 265(264). Row of basal asperities on S9 broadly interrupted at middle (Fig. 35.18Y); urogomphi with single pit between them. Under bark, in rotten stems ..... **Salpingidae**-OTHNIINAE (p. 669)
- Row of basal asperities on S9 more or less continuous (Fig. 35.18X); urogomphi with 2 pits between them. Under bark ..... **Pythidae**-PILIPALPINAE (p. 668)
- 266(210). Ratio of antennal length to head width less than 0.5; abdominal terga with paired rows of asperities forming incomplete rings (Fig. 35.18E); posterior edge of head capsule distinctly emarginate dorsally; labial palps 2-segmented. Under bark, in leaf axils ..... **Mycteridae**-LACCONOTINAE (p. 668)
- Ratio of antennal length to head width more than 0.5; abdominal terga without rows of asperities; posterior edge of head capsule not or only slightly emarginate dorsally; labial palps 1-segmented. In leaf axils ..... **Mycteridae** (*Hemipeplus*) (p. 668)

### Conventions used in Family Diagnoses

#### ADULT

ABD	Number of ventrites and in ( ) number of basal ventrites connate
ANT	Number of antennal segments and in ( ) antennal type or number of club segments
CLOS	Externally closed fore coxal cavities
(CLOS)	Internally closed fore coxal cavities (FCAV)
(CLOS)	Mid coxal cavities closed by meeting of sterna (MCOX)
(CON)	Trochantin concealed
CONT	Mid coxae contiguous
(EXP)	Trochantin at least partly exposed
FCAV	External and in ( ) internal closure of fore coxal cavities
FCOX	Shape of visible portion of fore coxa and in ( ) condition of trochantin
(FIL)	Filiform antennae
(FLAB)	Flabellate antennae
GLOB	Fore coxae globular and not projecting
(INCR)	Incrassate antennae
MCOX	Separation of mesocoxae and in ( ) lateral closure of mesocoxal cavity
(MON)	Moniliform antennae
NARR	Separated by less than 0.4 times coxal width (MCOX)
OPEN	Externally open fore coxal cavities
(OPEN)	Internally open fore coxal cavities (FCAV)
(OPEN)	Mid coxal cavities partly closed by mesepisternum (MCOX)
P3-3-3	Pseudotrimerous tarsi (see p. 547)
P4-4-4	Pseudotetramerous tarsi (see p. 547)
(PECT)	Pectinate antennae
PROJ	Fore coxae projecting below prosternum
(SER)	Serrate antennae
TRANS	Fore coxae transverse
VWIDE	Mid coxae separated by more than 1 coxal width
WIDE	Mid coxae separated by 0.4–1 times coxal width
5-5-5 etc.	Tarsal segments on each leg

#### LARVA

AB	Annular-biforous spiracles
AM	Annular-multiforous spiracles
AN	Annular spiracles
ANT	Number of antennal segments
AU	Annular-uniforous spiracles
BI	Biforous spiracles (with ecdysial scar)



CR	Cribriform spiracles
FR	Labrum free
FSUT	Frontoclypeal suture
FU	Labrum completely fused to head capsule
GLAC	Maxilla with galea and lacinia
HEAD	Orientation of head and in ( ) whether head retracted into thorax
HRD	Hypostomal rods
HSC	Hypopharyngeal sclerome
HYPO	Head hypognathous
LABR	Labrum (free or fused)
LEG	Number of leg segments
LP	Number of labial palp segments
MALA 0	Maxilla without lobes
MALA	Maxilla with single mala
MOLA	Mandibular mola
MP	Number of maxillary palp segments
PF	Labrum partly fused to head capsule
PRO(PRO)	Head prognathous and protracted
PRO(RET)	Head prognathous and retracted
PS	Sub-basal pseudomola
RED	Reduced and non-functional spiracles
SP	Spiracles of special type
SPIR	Type of abdominal spiracle
STEM	Number of stemmata on each side
TC	Number of tarsal claws
TS	Number of tarsungular setae
UROG	Urogomphi on T9
VER	Ventral epicranial ridges
VMP	Ventral mouth-parts or maxillolabial complex

For all characters, + = present, 0 = absent, R = rare, A = apparent (as in an apparently 2-segmented antenna with a minute 3rd segment (2A/3), - = to, / = or, ♂ = all males, ♂\* = males of some species, M = many (more than 12 for adult antennae, more than 5 for larval antennae, more than 2 for tarsungular setae). MM = body length in millimetres.

### Suborder ARCHOSTEMATA

Archostemata share with members of the Myxophaga and Adephaga the presence of an external prothoracic pleuron, the absence of cervical sclerites, and a type of hind wing which usually has a distinct oblongum cell and is folded so that the major transverse fold crosses the MP (see p. 550). As in Myxophaga, the apex of the wing is spirally rolled (Fig. 35.5B). In contrast to Adephaga, adults have movable hind coxae, usually with visible trochantins, and 5 (rather than 6) ventrites, and known larvae are wood boring, with large mandibular molae and a sclerotised ligula. In Cupedidae, the testes are not tubular and there are 4 Malpighian tubules. Myxophaga differ in having the larval tarsus and pretarsus fused to form a tarsungulus and in a suite of larval and adult adaptations to an aquatic or riparian existence. The suborder includes three families: Micromalthidae, which is native to North America but introduced in various parts of the world, Cupedidae and Ommatidae; the last group, however, was subdivided by Crowson (1976), with the minute, interstitial *Crowsoniella relict*a from Italy and the South American *Tetraphalerus* forming a separate family, Tetraphaleridae. Archostemata were common in the Mesozoic, and species of *Omma* and *Tetraphalerus* are known from Jurassic deposits. [Crowson 1975, 1976; Lawrence *et al.* 1987; Pace 1976; Ponomarenko 1969b]

**1. Ommatidae** (Fig. 35.19A). ADULT: ANT 11(FIL), FCOX GLOB(EXP), FCAV OPEN(OPEN), MCOX CONT(OPEN), 5-5-5, ABD 5(0), 7-26 MM. LARVA: UNKNOWN.

This family includes the Australian genus *Omma*, the South American *Tetraphalerus*, and *Crowsoniella relict*a from Italy. Australian ommatids may be distinguished from Cupedidae by the shorter, laterally inserted antennae, reduced labrum, tridentate mandibles, contiguous fore coxal cavities, and simple 4th tarsal segment, and by lacking ventral grooves for the reception of the legs. There are three described species, but they are rarely collected. Two occur in eastern Australia (*O. mastersi*, 7 to 11 mm long, clothed with flat, white and brown scales and *O. stanleyi*, 13-25 mm long, clothed with stout, decumbent setae), and a third is known from southern W.A. (*O. sagitta*, 10 mm and similar to *mastersi* but with the light scales forming an X on the combined elytra). [Neboiss 1960, 1989]

**2. Cupedidae** (Figs 35.19B-E). ADULT: ANT 11(FIL), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX CONT(OPEN), 5-5-5, ABD 5(0), 6-17 MM. LARVA: HEAD PRO(PRO), STEM 0, ANT 4/5, FSUT +, LABR FR, MOLA +, VMP RET, GLAC, MP 3, LP 2, HSC +, HRD +, VER 0, LEGS 6, TC 1/2, UROG 0, SPIR AN.

Distinguished from *Omma* by the unidentate mandibles

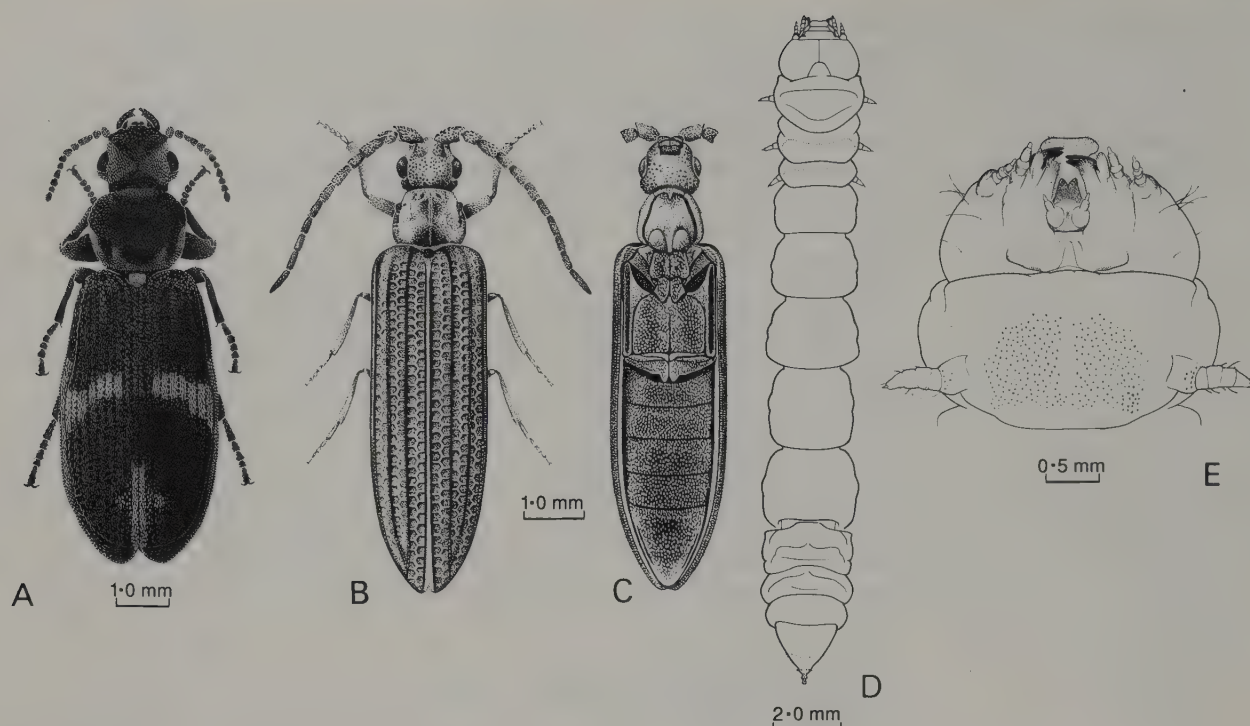


Fig. 35.19 Archostemata: A, *Omma mastersi*, Ommatidae. Cupedidae: B, *Distocupes varians*, dorsal; C, same, ventral; D, *D. varians*, larva, dorsal; E, same, head and prothorax, ventral. [A by B. P. Moore, after Moore 1982; B, C by F. Nanninga; D, E by A. Klinkenberg]

(with an additional subapical tooth) and by characters given in the family key (couplet 9, p. 567). Body more flattened and always clothed with flattened scales; elytra with rows of large, subquadrate *window punctures* (deep punctures with very thin, translucent cuticle at the bottom). Larvae lightly sclerotised, eruciform, with short legs and median spine on T9; head with long, median endocarina; mandibles robust with transversely ridged molae; labium with unique sclerotised ligula.

Cupedidae are known from all continents and most large islands, including New Caledonia (but not New Zealand). In Australia, *Distocupes varians* is distributed from Tas. to southern Qld, while *Adinolepis* (5 spp.) occurs in the south-east (as far west as Adelaide), northern Qld, and south-western W.A. Cupedid larvae bore into dead wood that has been previously attacked by fungi, but they may occur in fairly dry habitats. Larvae of *D. varians* have been collected in structural timber in Canberra. [Neboiss 1968, 1984, 1987a]

### Suborder MYXOPHAGA

This small group of minute beetles includes four families: Torridincolidae, Cyathoceridae, Hydroscaphidae and Microsporidae. Crowson (1960) considered this taxon to be the sister group of Polyphaga, based mainly on the fusion of the larval tarsus and pretarsus; Lawrence and Newton (1982) and Ponomarenko (1971) suggested that Recent Myxophaga may be descendants of the schizophoroid Archostemata (especially the family Catiniidae), which occurred in the Triassic and Jurassic. Myxophaga occur in various aquatic or riparian situations, such as in mud or sand in and at the edges of

streams and ponds, in hot springs (some *Hydroscapha* only), and on the surfaces of rocks which are covered with a moving film of water or constantly sprayed by waterfalls. Adults (e.g. in Torridincolidae) may have a ventral plastron (Hinton 1969), and all known larvae possess *spiracular gills* (tracheal gills) (Hinton 1967a). Cyathoceridae are distributed from Mexico to South America; Torridincolidae occur in South America, Africa, Madagascar and Japan; and Hydroscaphidae and Microsporidae are relatively widely distributed, the latter occurring in Australia. [Lawrence *et al.* 1987; Reichardt 1973; Satô 1982; Spangler 1980]

**3. Microsporidae** (Sphaeriidae; Figs 35.20A–C). ADULT: ANT 11(3), FCOX GLOB(EXP), FCAV OPEN (OPEN), MCOX CONT(OPEN), 3-3-3, ABD 3(0), 0.8–1.0 mm. LARVA: HEAD HYPO, STEM 4, ANT 2, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0, VER 0, LEGS 5, TS 1, UROG 0, SPIR AN.

Minute, globose, strongly convex and shining beetles distinguished from other Australian Coleoptera by having only 3 abdominal ventrites, compact antennal club, visible propleuron, and large coxal plates covering hind femora. The hind wing (Figs 35.5D, E) is fringed with long hairs (as in Ptiliidae), but the venation and folding are of the adephagan type, with a large oblongum cell and distinct medial hinge, while the apex is spirally rolled, as in Archostemata. Larvae (Figs 35.20B, C) broadly ovate with large, strongly declined, triangular head, large labrum covering mandibles and vesicular spiracular gills on abdominal segments 1–8. The family includes the single genus *Microsporus* (= *Sphaerius*, I.C.Z.N. Opinion



1331, Melville 1985), which occurs throughout the Northern Hemisphere and in Madagascar and Australia. The 2 described Australian species occur in N.S.W. and Vic. and in northern Qld. Both adults and larvae occur in wet mud and gravel at the edges of streams, where they probably feed on algae. The adult has no plastron but stores air beneath the elytra. [Britton 1966; Hinton 1967a]

### Suborder ADEPHAGA

The Adephaga is a relatively large group of highly specialised beetles, which differ from Archostemata and Myxophaga in having immobile hind coxae, 6 abdominal ventrites (the first of which is divided by the hind coxae) and pygidial defence glands in the adult, and liquid-feeding mouth-parts, with a fused labrum and no mandibular molae, in the larva. Four Malpighian tubules; testes tubular, coiled; ovarioles polytrophic. The vast majority of species are predacious, exceptions being the mycophagous Rhysodidae, the algophagous Haliplidae and Noteridae, and some phytophagous species among the harpaline Carabidae.

Adephaga have been the subjects of several major comparative anatomical studies [e.g. Forsythe (1982) and Evans and Forsythe (1985) on the adult feeding system; Hlavac (1971) and Regenruss (1975) on the antenna cleaner; Baehr (1979), Bell (1966, 1967), Beutel (1986), Beutel and Belkaceme (1986), M. E. G. Evans (1977, 1985), Hlavac (1972, 1975) and Larsén (1966) on the thorax; Hammond (1979) and Ward (1979) on the hind wing; Forsyth (1968, 1970, 1972) on the pygidial glands; Bils (1976) and Burnmeister (1976, 1980) on the ovipositor; Ruhnau (1986) on larval morphology]. In addition the chemistry of defensive secretions has been studied comparatively by B. P. Moore (1979) and Dettner (1985). These studies have often been accompanied by cladograms or have stimulated new phylogenetic hypotheses (see below). Traditionally, the suborder has been divided into Geadephaga and Hydradephaga, comprising the terrestrial and aquatic forms, respectively; however Trachypachidae (including the Holarctic *Trachypachus* and the Chilean *Systolosoma*) have the diagnostic adult features of the Hydradephaga combined with a terrestrial carabid-like larva. Furthermore, trachypachids are among the earliest Adephaga in the fossil record, occurring in the Triassic along with haliplid- and gyridid-like forms (Ponomarenko, in Arnoldi *et al.* 1977). M. E. G. Evans (1982, 1985) suggested that aquatic Adephaga may have arisen three times (Haliplidae, Gyrididae, remaining Hydradephaga) from a terrestrial ancestor, and the Triassic eodromeine Trachypachidae gave rise to both aquatic dytiscoids (Hygrobiidae, Amphizoidae, Noteridae, Dytiscidae) and all modern terrestrial Adephaga. Ponomarenko (in Arnoldi *et al.* 1977) presented a similar scheme, but considered the ancestral adephagans to have been aquatic. Other workers have proposed phylogenies in which Trachypachidae is the sister group of all Hydradephaga (Bell 1966, 1967; Ruhnau 1986) or Hydradephaga excluding the Haliplidae (Beutel and Belkaceme 1986; Roughley 1981); while Nichols (1985) considered Trachypachidae and all aquatic groups to form the sister

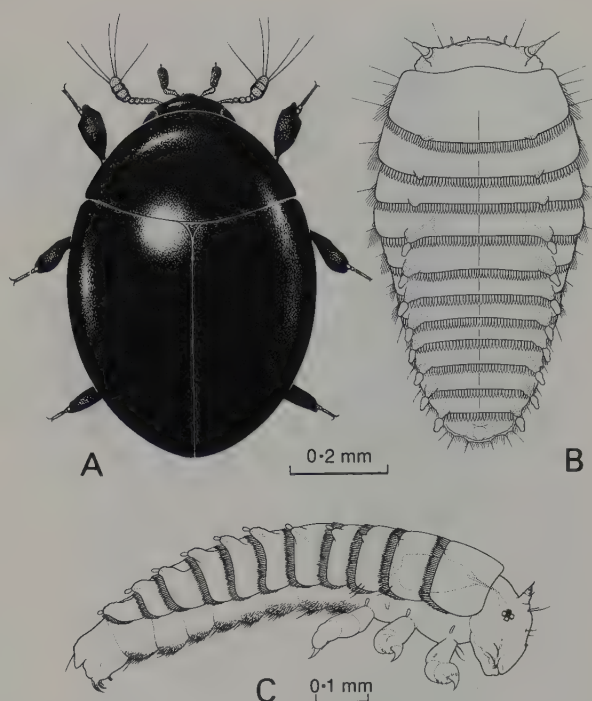


Fig. 35.20 Myxophaga: *Microspor ovensis*, Microsporidae: A, adult; B, larva, dorsal; C, larva, lateral. [F. Nanninga]

group of the genus *Omophron*, which, in turn, was placed within a derivative group of the family Carabidae.

The Australian Adephaga have been catalogued by Lawrence *et al.* (1987) and B. P. Moore *et al.* (1987); and Watts (1985) has discussed the Australian Hydradephaga.

**4. Rhysodidae** (Fig. 35.21A). ADULT: ANT 11 (MON), FCOX GLOB(CONC), FCAV CLOS(OPEN), MCOX MWIDE(OPEN), 5-5-5, ABD 6(3), 4.8-10 mm. LARVA: HEAD PRO(PRO), STEM 0, ANT 4, FSUT 0, LABR FU, MOLA 0, VMP RET, MALA, MP 3, LP 1, HSC 0, HRD +, VER 0, LEGS 6, TC 1, UROG 0, SPIR AN.

Black and shiny, subcylindrical to slightly flattened beetles with stout, moniliform antennae and deep grooves on head and pronotum (and sometimes elytra and abdomen), which may be lined with very fine pilosity and are often filled with dried organic material. Legs relatively short, with weakly developed antenna cleaner on fore tibia; metasternum without transverse suture; mouth-parts more or less concealed beneath expanded mentum; head strongly constricted posteriorly to form narrow neck. Larvae elongate, somewhat flattened and lightly sclerotised with short legs, no urogomphi, and transverse rows of asperities or interrupted ridges on T1 to 6 or 7; maxillae and labium reduced and usually clothed with fringed membranes. Both adults and larvae live in old, decayed logs and are thought to be associated with Myxomycetes. Although usually recognised as a distinct Adephagan lineage, Rhysodidae is sometimes placed within the family Carabidae, based on the presence of tactile setae, a carabid-like antenna cleaner, and structures of the pygidial defence system (Bell and Bell 1962; Forsyth 1972). The family is represented in Australia by endemic

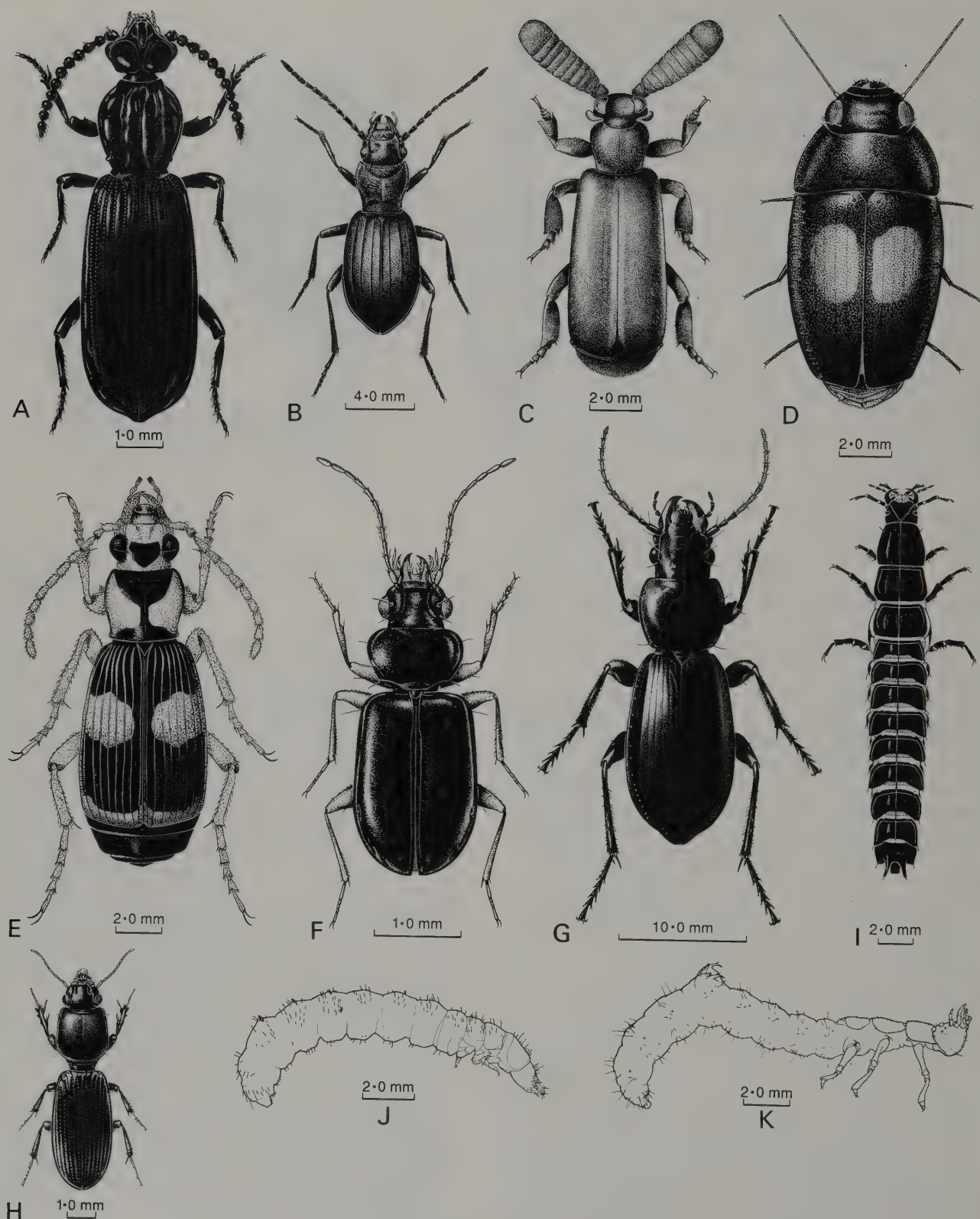


Fig. 35.21 Terrestrial Adephaga: A, *Leoglymmius lignarius*, Rhysodidae; B–H, Carabidae, adults: B, *Mystropomus subcostatus*, Ozaenini; C, *Arthropterus* sp., Paussini; D, *Sphallomorpha biplagiata*, Pseudomorphae; E, *Pheropsophus verticalis*, Brachininae; F, *Trechodes bipartitus*, Trechini; G, *Notonomus* sp., Pterostichini; H, *Clivina basalis*, Scaritini; I–K, Carabidae, larvae: I, *Pamborus macleayi*, Cychrini; J, *Sphallomorpha colymbetoides*, Pseudomorphae; K, *Cicindela* sp., Cicindelinae.  
[A–D, F, G by F. Nanninga; E, I after Moore 1982; H by T. Nolan; J after Moore 1974; K by A. Klinkenberg]



groups (*Leoglymmius*), as well as Melanesian intrusions (Bell 1985). Most of our species are in the genera *Kaveinga* and *Rhyzodiastes*. [Bell and Bell 1978, 1979]

**5. Carabidae** (ground beetles; Figs 35.21B–K; Plate 4, A, B, S). ADULT: ANT 11/10R(FIL/SERR/9R), FCOX GLOB(CONC), FCAV OPEN–CLOS(OPEN–CLOS), MCOX NARR–MWIDE(OPEN–CLOS), 5-5-5, ABD 6(3), 1.0–60 (2.5–35) MM. LARVA: HEAD PRO(PRO), STEM 0–6, ANT 2R/4, FSUT 0, LABR FU, MOLA 0, VMP PRO, GLAC/MALA, MP 3–5, LP 2/3, HSC 0, HRD 0, VER 0, LEGS 3–4R/6, TC 1/2, UROG 0R/+, SPIR AN.

A large group of active, cursorial, primarily carnivorous beetles with prominent mandibles and palps, a shortened metasternum with a distinct transverse suture, usually striate elytra and long, slender legs, and a characteristic series of punctures of fixed position bearing tactile setae. Except for the Paussini, carabids have an antenna cleaning organ, consisting of an excavation lined with a comb-like setal fringe located near the apex of the fore tibia (Figs 35.21F–H). Carabid antennae (except those of Paussini and some Pseudomorphinae) are more or less uniformly pubescent beginning at the 3rd, 4th or 5th segment. Many ground beetles are black and shiny, but others are brightly coloured or metallic and a few are pubescent. Larvae (Figs 35.13D, 21I) campodeiform, with well-developed legs, prominent antennae and mandibles, and almost always fixed urogomphi, which may be segmented.

As a dominant group of terrestrial predators, Carabidae occur in a wide variety of habitats. Darlington (1961a, 1971) placed them in three main ecological groups: *geophiles* or *mesophiles*, which live on the ground but are not associated with water, *hydrophiles* living at the edges of streams or ponds or in swamps, and *arboricoles* living above the ground on tree trunks, logs or leaves. The proportion of geophiles: hydrophiles: arboricoles in the Australian fauna was found to be 2:1:1; in Papua New Guinea the ratio was closer to 1.2:1:1.

The classification of Carabidae has received a great deal of attention in the past 20 years, and there are still major problems to be solved at all levels (Ball 1979). The system used here follows that of B. P. Moore *et al.* (1987), which is based on that of Kryzhanovsky (1976).

#### Key to the Subfamilies and Tribes of Carabidae known in Australia

1. Antennal scape not visible from above (Fig. 35.21D); antennae sometimes short and clavate; head with deep antennal sulcus between eye and mandible; legs more or less concealed beneath body, which may be flattened and laterally explanate ..... PSEUDOMORPHINAE
- Antennal scape visible from above; antennae never short and clavate; antennal sulcus absent or shallow; legs not concealed beneath body ..... 2
- 2(1). Abdomen with 7 or 8 ventrites; elytra truncate, exposing 1 abdominal tergite (Fig. 35.21E); mandible with setiferous puncture in concavity

- (scrobe) along outer edge; head with 1 pair of supraorbital setiferous punctures ..... BRACHININAE
- Abdomen with 6 ventrites; without other characters in combination ..... 3
- 3(2). Clypeus broader than distance between antennal sockets; eyes large and protruding; legs very long and slender; fore tibia with 2 spurs terminal; lateral pronotal carinae absent or incomplete posteriorly ..... CICINDELINAE
- Clypeus narrower than distance between antennal sockets; without other characters in combination ..... 4
- 4(3). Fore tibia with 2 spurs terminal, independent of antenna cleaner, which may be absent; mid coxal cavities open laterally (partly closed by mesepimeron) (Fig. 35.6A) ..... (PAUSSINAE) 5
- Fore tibia with outer spur placed closer to apex than inner spur, the 2 spurs located on either side of antenna cleaner, which is always present ..... (CARABINAE) 6
- 5(4). Antennae 11-segmented and filiform; tibiae not flattened; elytra not truncate; antenna cleaner present; labial palps fusiform ..... Ozaenini
- Antennae apparently 10-segmented (pedicel enclosed within scape) and flattened, the segments strongly expanded and plate-like or rarely serrate; tibiae flattened; elytra truncate, exposing 1 or 2 tergites; antenna cleaner absent; labial palps strongly securiform ..... Paussini
- 6(4). Metepimeron not visible between posterior edge of metepisternum and anterior edge of first ventrite; mid coxal cavities open laterally, partly closed by mesepimeron (Fig. 35.6A) ..... 7
- Metepimeron visible as lobe between metepisternum and first ventrite; mid coxal cavities usually closed laterally by meeting of sterna (Fig. 35.15w) ..... 9
- 7(6). Fore coxal cavities closed behind (Fig. 35.15Q); apical segment of maxillary palp slender and fusiform; length less than 15 mm ..... Migadopini
- Fore coxal cavities open behind (Fig. 35.15O); apical segment of maxillary palp more or less expanded and truncate apically; length more than 15 mm ..... 8
- 8(7). Mandibles multidentate, their upper surfaces smooth; clypeus without setiferous punctures ..... Cychnini
- Mandibles not toothed, their upper surfaces rugose; clypeus with setiferous puncture at each anterior angle ..... Carabini
- 9(6). Body pedunculate, with a distinct, narrow waist or peduncle between prothorax and elytra, the scutellum entirely contained within peduncle ..... 10
- Body not pedunculate, or if slightly so, then scutellum extending behind peduncle and forming a wedge between elytral bases ..... 13
- 10(9). Mid coxal cavities open laterally, partly closed by mesepimeron (Fig. 35.6A) ..... 11
- Mid coxal cavities closed laterally by meeting of sterna (Fig. 35.15w) ..... 12
- 11(10). Antennal scape with subapical setiferous puncture ..... Clivinini

- Antennal scape without setiferous puncture ..... Scaritini
- 12(10). Body pubescent; prothorax globular, without well-defined lateral carinae; palps long and slender ..... Apotomini
- Body glabrous; prothorax with well-defined lateral carinae; palps normal ..... Broschini
- 13(9). Mandible with one setiferous puncture in concavity (scrobe) along outer edge (Fig. 3.5) ..... 14
- Mandible without setiferous puncture in scrobe (or in Helluonini with several setiferous punctures) ..... 18
- 14(13). Bases of elytra with complete, well-defined margins; tarsi without setae beneath; marginal series of 12 setiferous punctures on elytra not divided into 2 groups; terminal segment of maxillary palp fusiform ..... Pogonini
- Bases of elytra without complete, well-defined margins; tarsi pubescent beneath; marginal series of 8 or 9 setiferous punctures on elytra divided into anterior group of 4 and posterior group of 4 or 5; terminal segment of maxillary palp usually conical or subulate (small and cylindrical) (Fig. 35.21F) ..... 15
- 15(14). Terminal segment of maxillary palp very small; frontal region with short furrows which never extend behind eyes ..... Bembidiini
- Terminal segment of maxillary palp usually about same length as penultimate segment, or if very small (*Perileptus*), then frontal furrows extending behind posterior edges of eyes ..... 16
- 16(15). Elytra without inner longitudinal ridge beneath apical edge; frontal furrows of head extending behind posterior edges of eyes (Figs 3.5; 35.21F) ..... Trechini
- Elytra with inner longitudinal ridge, the end of which is visible beneath edge of elytron, level with apical end of epipleuron; frontal furrows of head not extending behind eyes ..... 17
- 17(16). Penultimate segment of maxillary palp setose; fore tarsi of male with 2 basal segments dilated and dentate on inner side ..... Zolini
- Penultimate segment of maxillary palp glabrous; fore tarsi of male not or only slightly modified ..... Psydrini
- 18(13). Base of fore femur with ventral boss or tubercle forming the proximal end of a flat or slightly concave, shiny surface, which fits against the antenna cleaner when the tibia is flexed (when boss is absent or poorly developed, the shiny surface is still present); labrum large and relatively long, usually longer than antennal scape, its apex strongly produced and rounded to subangulate; elytral apices almost always subtruncate; large species, rarely less than 12 mm in length, almost always black or metallic blue in colour ..... Helluonini
- Fore femur without ventral tubercle at base; without other characters in combination ..... 19
- 19(18). Elytral apices rounded so that they form a single curve, or acutely angled at apex; abdominal apex usually concealed from above; colour rarely yellow and black or metallic blue ..... 20
- Elytral apices transversely or obliquely truncate, exposing abdominal apex from above; colour often yellow and black or metallic blue; body often flattened or with elongate, narrow prothorax ..... 33
- 20(19). Head strongly constricted posteriorly to form narrow neck; pronotum slightly longer than wide, strongly constricted posteriorly, and less than half as wide at base than elytra; all tarsi lobed and densely pilose beneath; Cape York Peninsula, Qld ..... Hexagoniini
- Without above characters in combination ..... 21
- 21(20). Head with 1 pair of supraorbital setiferous punctures ..... 22
- Head with 2 pairs of supraorbital setiferous punctures ..... 26
- 22(21). Antennae densely pubescent from middle of 3rd segment onwards ..... Harpalini
- Antennae densely pubescent from base of 4th segment onwards ..... 23
- 23(22). Elytron without inner carina visible below lateral edge; apical segment of labial palp strongly dilated and broadly triangular ..... Agonicini
- Elytron with inner carina the apical end of which is visible below lateral edge towards apex, causing epipleuron to appear twisted; apical segment of labial palp not broadly triangular ..... 24
- 24(23). Elytra usually densely pubescent (sometimes glabrous except along lateral edges); colour often metallic ..... Callistini
- Elytral surface more or less glabrous, never densely pubescent; colour black ..... 25
- 25(24). Pronotum distinctly narrowed basally, its basal width much less than that of combined elytral bases; 8th elytral stria normal, not forming deep channel ..... Pterostichini (*Abacetus*)
- Pronotum not narrowed basally, its basal width about equal to that of combined elytral bases; 8th elytral stria forming deep channel parallel to outer edge ..... Oodini
- 26(21). Apical segment of labial palps strongly securiform; body coarsely punctate and densely pubescent ..... Panagaeini
- Apical segment of labial palp not strongly securiform; body not coarsely punctate and densely pubescent ..... 27
- 27(26). Elytra with sparse, short pubescence on depressed marginal area outside 8th stria, remainder of elytral surface smooth, glabrous and shining, with striae very faint or absent ..... Perigonini
- Elytra without pubescence outside 8th stria; striae visible on disc of elytra ..... 28
- 28(27). Clypeus almost always emarginate and sometimes asymmetrical; pale membrane present between clypeus and labrum (usually within emargination); mandibles characteristically bifurcate, with large mesal tooth; labrum often deeply emarginate; length less than 25 mm ..... Licinini
- Clypeus not emarginate, never asymmetrical and without an obvious pale membrane between it and labrum (except in *Mecynognathus*, where the length is greater than 30 mm and the mandibles are simple) ..... 29



- 29(28). Elytron with inner longitudinal carina the apical end of which is visible below lateral edge towards apex, causing end of epipleuron to appear twisted (inner carina sometimes concealed by lateral edge of abdomen, which fits into groove between it and epipleural apex); mentum usually bifid at apex ..... 30
- Elytron without inner carina visible below lateral edge (carina may be present but does not extend to lateral edge); mentum usually simple or with a single median tooth at apex ..... 31
- 30(29). Antennae with 4 basal segments glabrous ..... Morionini
- Antennae with only 3 basal segments glabrous ..... Pterostichini (major part)
- 31(29). Outer edges of mandibles markedly curved; dorso-lateral carina projecting laterally farther than ventrolateral one, so that scrobe is concealed from above. .... Masoreini
- Outer edges of mandibles normally curved, dorso-lateral carina not projecting beyond ventrolateral one ..... 32
- 32(31). Elytra with scutellary striole; length less than 20 mm; body relatively slender and more or less flattened above ..... Agonini (major part)
- Elytra without scutellary striole OR length greater than 25 mm; body usually stouter and more convex ..... Pterostichini
- 33(19). Labial palps greatly enlarged and securiform; eyes reduced and crescent-shaped; antennae short and moniliform ..... Leleupidiini
- Labial palps not greatly enlarged and securiform; eyes larger and rounded; antennae longer and filiform or flattened ..... 34
- 34(33). Antenna densely pubescent from base; scape much longer than other segments, usually at least 3 times as long as pedicel ..... 35
- Antenna densely pubescent from segment 4 or 5, basal segments each with 1 or 2 setae only; scape shorter, usually less than 2.5 times as long as pedicel ..... 37
- 35(34). Prothorax subcylindrical, without or with very weak lateral carinae; scape more than 8 times as long as pedicel; penultimate tarsal segment deeply bilobed ..... Dryptini
- Prothorax with sharp lateral carinae; scape less than 7 times as long as pedicel; penultimate tarsal segment not deeply bilobed ..... 36
- 36(35). Antennal scape shorter than following 2 segments combined; elytral intervals moderately convex, never costate ..... Physocrotaphini (*Pogonoglossus*)
- Antennal scape usually longer than following 3 segments combined; if shorter, then elytra each with 1 distinct costa or more than 20 fine costae ..... Zuphiini
- 37(34). Prothorax subcylindrical, without or with obsolete or sublateral carinae ..... Odacanthini
- Prothorax with sharp lateral carinae, not subcylindrical ..... 38
- 38(37). Prothorax subquadrate, not or very slightly narrowed posteriorly; base of pronotum less than half as wide as combined elytral bases; tarsal segment 4 deeply bilobed; tarsal claws pectinate; Tas. .... Ctenodactylini (*Plagiotelum*)
- Without these characters in combination ..... 39
- 39(38). Hind tibiae with unusually long spurs ..... Tetragonoderini
- Hind tibiae with spurs of normal length ..... 40
- 40(39). Pronotum strongly constricted posteriorly; lateral edge of pronotal disc with a single setiferous puncture; elytra narrowed at base, their humeri strongly produced and rounded anteriorly; galea 1-segmented ..... Agonini (*Homethes*)
- Without above characters in combination ..... 41
- 41(40). Mentum supported on projecting submentum; head not sharply constricted behind eyes; mandible with outer hollow face; claws often pectinate ..... Lebiini
- Without projecting submentum; head sharply constricted behind eyes; mandible without hollow outer face; claws simple ..... Pentagoniciini

Australian PAUSSINAE (Figs 35.21B, C) includes two tribes, Ozaenini and Paussini, which are very different in appearance, but which share a unique type of crepitating system, and lack a number of features which characterise the more derived carabid groups. Ozaenini are represented by a few species of *Mystropomus*, occurring mainly in coastal rainforests of N.S.W. and Qld; these have filiform antennae, slender legs and fixed tactile setae, as in most Carabidae, and a primitive type of antenna cleaner. The Australian Paussini include the North Qld *Megalopaussus amplipennis*, which has been found in the nest of the ant *Notostigma* sp., and the large genus *Arthropterus*, which is distributed throughout Australia, especially in more arid regions, and also contains several species which have been associated with ants (Lea 1910a). Adult Paussini are unique in the family for having flattened legs, flattened and serrate or club-like, apparently 10-segmented antennae (having the pedicel concealed within the scape) and no antenna cleaner or tactile setae. Larvae of both tribes have a highly modified, disc-like abdominal apex (Bousquet 1986).

CICINDELINAE (tiger beetles, Plate 4, A) are usually brightly coloured, with a deflexed head, large labrum, large protruding eyes, long, slender legs and non-striate elytra. Adults of most species are capable of running and flying rapidly in open areas, such as river banks, beaches, forest clearings and salt pans, but others occur on tree trunks and may be wingless. Larvae (Fig. 35.21k) are highly modified ambush predators living in vertical tunnels in the soil or sometimes in wood; they lack urogomphi, have a flattened head which serves as a lid or plug, and are armed with 2 or 3 pairs of dorsal abdominal hooks, which serve to anchor them in the tunnel. *Cicindela* inhabits sandy heaths, beaches, sand banks or salt pans and is active in daylight, while *Megacephala* has a striking metallic green, blue or violet colour, and is nocturnal. *Dystipsidera* and *Rhysoleura* are active on tree trunks, as is the wingless, black *Tricondyla aptera*, which is distributed from Cape York to the Moluccas and

Vanuatu. Tiger beetle biology was reviewed by Pearson (1988), Australian *Cicindela* were revised by Freitag (1979), and the subgenera of *Cicindela* were treated by Sumlin (1982).

Of the more than 500 known species of bombardier beetles (BRACHININAE), only one, *Pheropsophus verticalis* (Fig. 35.21E), occurs in Australia; the species is widespread and extends into Papua New Guinea and the Solomon Islands, while the genus occurs over much of Africa, Asia and Melanesia (Erwin 1970). Adults are black with yellow spots, and when disturbed, they emit a small cloud of visible vapour from the abdominal apex, accompanied by an audible 'pop' (p. 92). The crepitating mechanism responsible for this defensive discharge and the chemistry of the spray are similar to that found in Paussinae (Aneshansley *et al.* 1983). Some larval Brachininae are known to be ectoparasitoids of beetle pupae, and the Japanese *Pheropsophus jessoensis* has been recorded preying on the egg masses of mole crickets (ORTH: Gryllotalpidae) (Habu and Sadanaga 1965).

PSEUDOMORPHINAE (Fig. 35.21D) are a predominantly Australian group of ovoid and sometimes strongly flattened beetles, whose antennae and legs may be completely concealed beneath the body when at rest. Adults of *Sphallomorpha* and *Silphomorpha* have filiform antennae as in most carabids, but in other Australian genera, such as *Adelotopus*, they are short and club-like. Larvae of *Sphallomorpha* (Fig. 35.21J) live in vertical tunnels at the periphery of ant nests, and, like cicindelids, they are ambush predators and have abdominal hooks to secure them in the tunnel (B. P. Moore 1974). Larvae of *Adelotopus* and the exotic *Pseudomorpha*, however, are physogastric inquilines in ant nests (Erwin 1981). An unusual feature in this subfamily is ovoviviparity, which has been reported for *Pseudomorpha* (Liebherr and Kavanaugh 1985).

The subfamily CARABINAE includes the remaining 32 tribes and the vast majority of Australian species. The primarily Northern Hemisphere tribes Carabini and Cydrini are represented in Australia by the world-wide genus *Calosoma* (Plate 4, B) and the autochthonous *Pamborus*, respectively. The former are widely distributed predators of caterpillars, while the latter feed on snails and earthworms in eastern coastal forests. Migadopini include a few species with southern temperate affinities, while Broscini are an amphipolar group (Crowson 1980), restricted to the temperate parts of both Northern and Southern Hemispheres; in Australia, migadopines are usually rare (although *Stichonotus* may be common in Tas.), while broscines are most widely distributed in arid and semi-arid regions. Scaritini, most diverse in drier areas, include large fossorial forms with modified digging fore tibiae (e.g. *Euryscaphus waterhousei*), as well as brilliantly metallic *Carenum* (Plate 4, S).

The Trechini and related groups are composed mainly of small to minute carabids, which are most abundant in the mountains of south-eastern Australia and Tas. They often frequent damp situations; *Perileptus constricticeps* is found in gravel at the edges of streams, and *Goedetrechus mendumae* (Fig. 3.5) is an eyeless, depig-

mented troglobite (B. P. Moore 1972). Bembidiini include some of the smallest carabids (*Illaphanus* spp.), while Zolini include the cave-inhabiting *Idacarus troglodytes*. The related tribes Morionini and Pterostichini form the largest group of typical, forest-dwelling geophiles in Australia. Among the morionines are gigantic forms, such as *Hyperion schroetteri*, which feeds on scarabaeoid larvae in rotten wood. *Notonomus* is common in coastal forests of eastern Australia, and like some other pterostichines, exhibits brood care (Brandmayr and Zetto Brandmayr 1979; B. P. Moore 1980). Harpalini are not as well represented in Australia as in other parts of the world. Harpaline larvae tend to be phytophagous, and their larvae have more heavily built mandibles than their predacious relatives. Lebiini include many small, flattened, yellow and black carabids common beneath loose bark or on bark and wood surfaces at night. Larvae of some exotic lebiines are predators or parasitoids on the pupae of other beetles (Erwin 1979). Although the habits of Australian Helluonini are unknown, exotic species are known to be associated with ants (Kistner 1982) or termites (J. C. M. Gardner 1933).

**6. Haliplidae** (Figs 35.22C, D). ADULT: ANT 11(FIL), FCOX GLOB(CONC), FCAV OPEN(CLOS), MCOX VWIDE(OPEN), 5-5-5, ABD 6(3), 2.5-3.6 MM. LARVA: HEAD PRO(PRO), STEM 2/6, ANT 4/5, FSUT 0, LABR FU, MOLA 0, VMP PRO, GLAC/MALA, MP 3, LP 2, HSC 0, HRD 0, VER 0, LEGS 6, TC 1, UROG 0, SPIR AN/RED.

Small, convex, boat-shaped beetles with large hind coxal plates, concealing basal abdominal ventrites and hind femora. Scutellum absent; elytra strongly, seriatly punctate; swimming hairs present on tibiae and tarsi. Larvae elongate and narrow, with 10 well-developed abdominal segments, the last of which forms long, narrow process. Mandibles short, stout and perforate, and in known Australian species thoracic terga and T1 to T9 each have 2 pairs of posteriorly projecting, spine-like processes. Spiracles lacking, except in final instar, and respiration takes place through microtracheal gills (Seeger 1971). Haliplids are found among aquatic vegetation at the edges of ponds, lakes or slow-moving streams; adults usually crawl along the bottom, but they are able to swim using alternate leg movements. Adult and larval haliplids commonly feed on stoneworts (Charophyceae) and some other kinds of green algae. The family occurs on all continents and Madagascar and is represented in Australia by *Haliphus*. [Watts 1988a]

**7. Hygrobiidae** (Figs 35.22A, B). ADULT: ANT 11(FIL), FCOX GLOB(CONC), FCAV OPEN(CLOS), MCOX NARR(OPEN), 5-5-5, ABD 6(3), 8-11.5 MM. LARVA: HEAD PRO(PRO), STEM 6, ANT 4, FSUT 0, LABR FU, MOLA 0, VMP PRO, MALA 0, MP 4, LP 2, HSC 0, HRD 0, VER 0, LEGS 6, TC 2, UROG +, SPIR AN/RED.

Stout and oval beetles with strongly protuberant eyes and relatively small hind coxae (not greatly enlarged like those of noterids, dytiscids and gyrids). Metasternum with transverse suture; tibiae and tarsi with swimming hairs. Larvae broadly fusiform, with enlarged head and



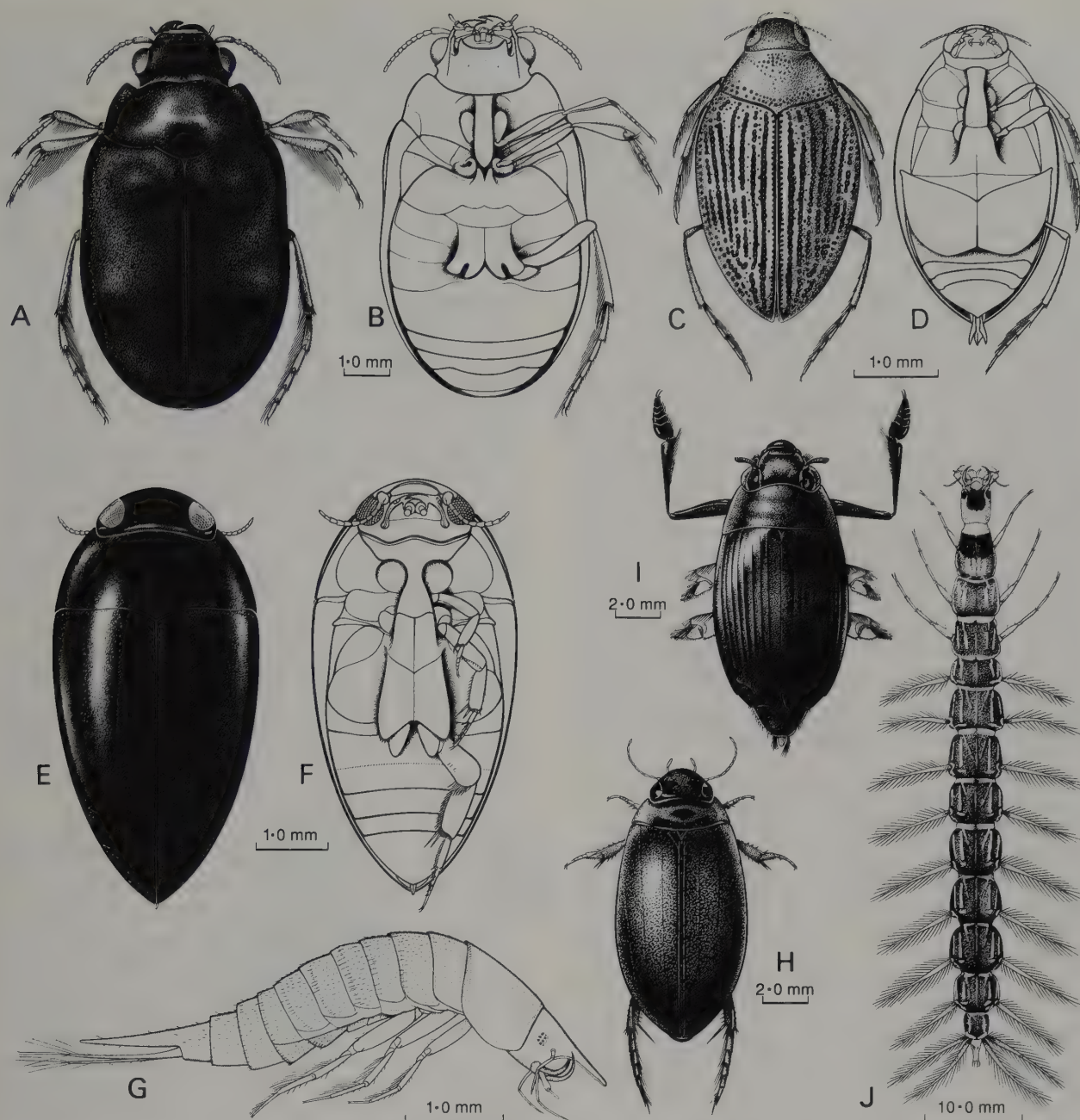


Fig. 35.22 Aquatic Adephaga: A, *Hygrobia nigra*, Hygrobiidae, dorsal; B, same, ventral; C, *Haliplus testudo*, Haliplidae, dorsal; D, same, ventral; E, *Hydrocanthus australasiae*, Noteridae, dorsal; F, same, ventral; G, Dytiscidae, Hydroporinae, larva; H, *Rhantus suturalis*, Dytiscidae; I, *Macrogyrus oblongus*, Gyrinidae; J, *M. striolatus*, larva. [F. Nanninga]

prothorax; mandibles falcate but not perforate; tibiae and tarsi with swimming hairs; paired gill tufts arising from coxal bases and S1–S3; apical abdominal segments reduced and modified; segment 8 with long and narrow median process; 9 with 2 long and narrow urogomphi, and 10 membranous; functional spiracles present in last instar only. Hygrobiids are relatively slow-moving, bottom-feeding predators, occurring in stagnant water. Adults swim using alternate leg movements, and periodically come to the surface for air, which is stored beneath the elytra. Adults stridulate using the abdominal

apex and a file on the undersurface of each elytron. Both adults and larvae are predacious, and the European *Hygrobia hermanni* is known to feed on tubificid worms (Balfour-Browne 1922). The family comprises five species of *Hygrobia*: one from western China, one from Europe and North Africa, and three from Australia. Two of the Australian species occur in the south-eastern part of the continent, while a third is known from the N.T. and Cape York Peninsula (Britton 1981).

**8. Noteridae** (Figs 35.22E, F). ADULT: ANT 11(FIL), FCOX GLOB(CONC), FCAV OPEN(CLOS), MCOX

NARR-MWIDE(OPEN), 5-5-5, ABD 6(3), 1.4-6 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 4, FSUT 0, LABR FU, MOLA 0, VMP PRO, MALA, MP 3, LP 2, HSC 0, HRD 0, VER 0, LEGS 6, TC 2, UROG +, SPIR AN/RED.

Adult noterids are distinguished from Dytiscidae by the greater convexity of the dorsal surface, longitudinally oriented, hind coxal plates, and absence of a scutellum (present in almost all dytiscids). Also, the prosternal process is moderately broad and abuts on the metasternum, forming with it and the hind coxal plates a flattened keel. Larvae with very compact, fusiform shape, short legs, very short urogomphi, and mandibles broad at base and non-perforate. As in Dytiscidae, the posterior spiracles are placed close together at the end of T8, which forms the apex of the abdomen. Noterids usually inhabit the margins of shallow ponds, where adults and larvae are commonly found among the roots of floating or emergent aquatic plants. Larvae of some species obtain air by tapping plants with the aid of the spiracle-bearing siphon at the end of the abdomen. Little is known of the feeding habits, but it is generally thought that noterids are detritus feeders. Known pupae are contained in air-filled cocoons attached to the roots of aquatic plants. The family is widely distributed throughout the warmer parts of the world, and the Australian species, belonging to the genera *Hydrocanthus*, *Canthydrus*, *Notomicrus* and *Hydrocoptus*, occur primarily in the northern part of the continent. [Balfour-Browne and Balfour-Browne 1940; Beutel and Roughley 1987]

**9. Dytiscidae** (predacious diving beetles; Figs 35.22G, H). ADULT: ANT 11(FIL), FCOX GLOB(CONC), FCAV OPEN(CLOS), MCOX CONT-MWIDE(OPEN), 5-5-5, ABD 6(3), 1.2-38 (3-32) mm. LARVA: HEAD PRO(PRO), STEM 0/6, ANT 4/5, FSUT 0, LABR FU, MOLA 0, VMP PRO, MALA, MP 3/4, LAB 2-4, HSC 0, HRD 0, VER 0, LEGS 6, TC 2, UROG +, SPIR AN/RED.

This is the largest and most commonly encountered group of aquatic Adephaga. Adults smooth and boat-shaped, with very large hind coxae (lacking coxal plates) and enlarged hind legs, which move synchronously in swimming and have flattened, paddle-like tarsi bearing a dense fringe of swimming hairs. Dorsal and ventral surfaces of body of similar convexity, with no median, flattened keel on the latter. Males in some groups have the first 3 segments of the fore tarsi greatly dilated to form adhesive pads equipped with suction discs, which are used to hold the female during copulation. Larvae with a relatively streamlined form, well-developed fringed swimming legs, large falcate mandibles, almost always deeply grooved or perforate, and 8th spiracles placed at end of elongate, siphon-like tergal process. Both adults and larvae come to the surface for air, which they obtain through the terminal pair of spiracles, and the former may store air beneath the elytra. Adults are normally capable of sustained, crepuscular or nocturnal flight, which is necessary for dispersal to isolated habitats; they are often attracted to lights and may mistake artificial shining surfaces, such as glass, for water.

Dytiscids inhabit a variety of lentic and some lotic freshwater habitats, but they are most abundant in the littoral zone at the edges of lakes and ponds. They may also occur in water-filled ditches, dams, billabongs, pools in intermittent streams, and even saline inland lakes. Both adults and larvae are predators on other aquatic animals, including insects, crustaceans, worms, leeches, molluscs, tadpoles or even small fish. Adults and some larvae are capable of taking in solid and liquid food through the mouth opening, but most larvae have a closed mouth opening and use the mandibular channels both for injecting digestive enzymes into the prey and for sucking in the resulting fluids, by means of a cibarial-pharyngeal pumping apparatus. Eggs are often deposited in slits made by the ovipositor in the stems of aquatic plants, but this habit is not universal. Pupation takes place in a cell formed by the larva in damp soil near, but out of, the water. All of the major groups of Dytiscidae occur in Australia, and the greatest number of species is found in the south-east. *Eretes australis* is a common and widespread inland species, while the largest Australian dytiscid, *Cybister godeffroyi*, occurs on Cape York Peninsula. *Terradessus caecus* is a blind, terrestrial species known only from high altitude rainforests in North Qld (Watts 1982). [De Marzo 1979; Galewski 1971; Watts 1963, 1964, 1978]

**10. Gyrinidae** (whirligig beetles; Figs 35.22I, J). ADULT: ANT 8-10(INCR/6-8), FCOX TRANS(EXP), FCAV OPEN(CLOS), MCOX NARR(OPEN), 5-5-5, ABD 7(3), 4-18 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 4, FSUT 0, LABR FU, MOLA 0, VMP PRO, GLAC, MP 4, LP 3, HSC 0, HRD 0, VER 0, LEGS 6, TC 2, UROG 0, SPIR AN/RED.

Adult gyrinids have the general streamlined appearance of Dytiscidae, but they are easily recognised by the fact that the eyes are completely divided into an upper and lower portion by a strip of cuticle and by their habit of swimming mainly on water surfaces. Antennae very short and compact; mid and hind legs short, flattened and paddle-like, with fringes of swimming hairs; fore legs long and slender, with expanded tarsi in males. Larvae elongate and slender, with falcate, perforated mandibles, 1 pair of lateral, feathery gills on each of first 8 abdominal segments, 2 pairs of gills on 9th segment, and 2 pairs of hooks at apex of 10th segment; functional spiracles absent except in last instar.

Gyrinidae inhabit both still and moving water. Adults are gregarious, usually active in daylight, and known for the way in which they gyrate, or swim in tight circles on the surface, with the aid of surfactants secreted by the pygidial glands (Vulinec 1987). They feed mainly on insects which have fallen into the water, and they locate prey using the Johnston's organ (located in the antennal pedicel), which is sensitive to surface waves. Larvae are bottom-feeding predators, which remain submerged and obtain oxygen through the abdominal gills; the final instar leaves the water to pupate within a cocoon. The family is widely distributed throughout the world and is represented in Australia by the genera *Gyrinus*, *Aulonogyrus*, *Dineutus* and *Macrogyrus*, the last of which includes our largest species. [Ochs 1949]



### Suborder POLYPHAGA

This is the largest and most diverse group of Coleoptera, containing more than 90% of the species and families. Members of the Polyphaga differ from those of the other three suborders in having the prothoracic pleuron fused with the trochantin and entirely concealed, forming a *cryptopleuron*, the hind wing without an oblongum cell and with the transverse fold never crossing MP, the cervical sclerites present and the ovarioles telotrophic. In addition, the metepisternum almost never meets the mid coxal cavity (rare exceptions occurring in Derodontidae) and the hind coxae are usually motile and do not divide the first ventrite. The earliest fossil definitely attributed to Polyphaga is *Peltosyne triassica* from the Triassic of Central Asia (Ponomarenko, in Arnoldi *et al.* 1977), but Crowson (1975) and Ponomarenko (1969b) have suggested that the archostematan family Ademosynidae may represent polyphagan ancestors in which the prothoracic pleuron has not yet become internalised.

### Series STAPHYLINIFORMIA

Staphyliniform adults are characterised by having reduced wing venation (except in Hydrophilidae) and a high grade type of wing folding mechanism which does not involve an intrinsic spring; larvae have articulated urogomphi in all but a few clearly derived taxa. The recognition of only two superfamilies, Hydrophiloidea and Staphylinoidea, and the inclusion of Hydraenidae in the latter are discussed by Lawrence and Newton (1982).

### Superfamily HYDROPHILOIDEA

Adults have relatively short antennae with long scape and 3-segmented, densely pubescent club, with segment preceding club transverse, concave, and in aquatic forms used to assist in replenishing air supply. Procoxae very large, legs often spinose or dentate, wings almost always with R-M loop and without spring mechanism, abdominal spiracles 7 or 7 and 8 atrophied, aedeagus of trilobed type (with fused parameres in most Histeridae), 6 free Malpighian tubules. Larvae predacious with large, protruding, falcate mandibles, no mola, fused labrum, maxillae almost always without apical lobes, maxillary palpifer complete and usually bearing articulated appendage, spiracles almost always biforous with closing apparatus and elateroid type of moulting process, abdomen largely membranous, and urogomphi relatively small and articulated or sometimes absent.

**11. Hydrophilidae** (Figs 35.23A–J). ADULT: ANT 7–9(1A/1R/3), FCOX TRANS–PROJ(EXP–CONC), FCAV OPEN–CLOS(CLOS), MCOX CONT–VWIDE(OPEN–CLOS), 5-5-5/4-4-4R, ABD 4R/5/6R(0-2), 0.9–42 (2–35) MM. LARVA: HEAD PRO(PRO), STEM 1A/6, ANT 3, FSUT 0, LABR FU, MOLA 0, VMP PRO/RETR., MALA 0/+R, MP 4, LP 1R/2, HSC 0, HRD 0. VER 0/+R, LEGS 0/3/5, TS 1/2/M, UROG 0A/0R/+R, SPIR BI/ANR/RED.

Most adults may be distinguished by the short, 7- to 9-segmented antennae, with a 3-segmented, pubescent club, preceded by a glabrous, cup-like segment (cupule) (Figs

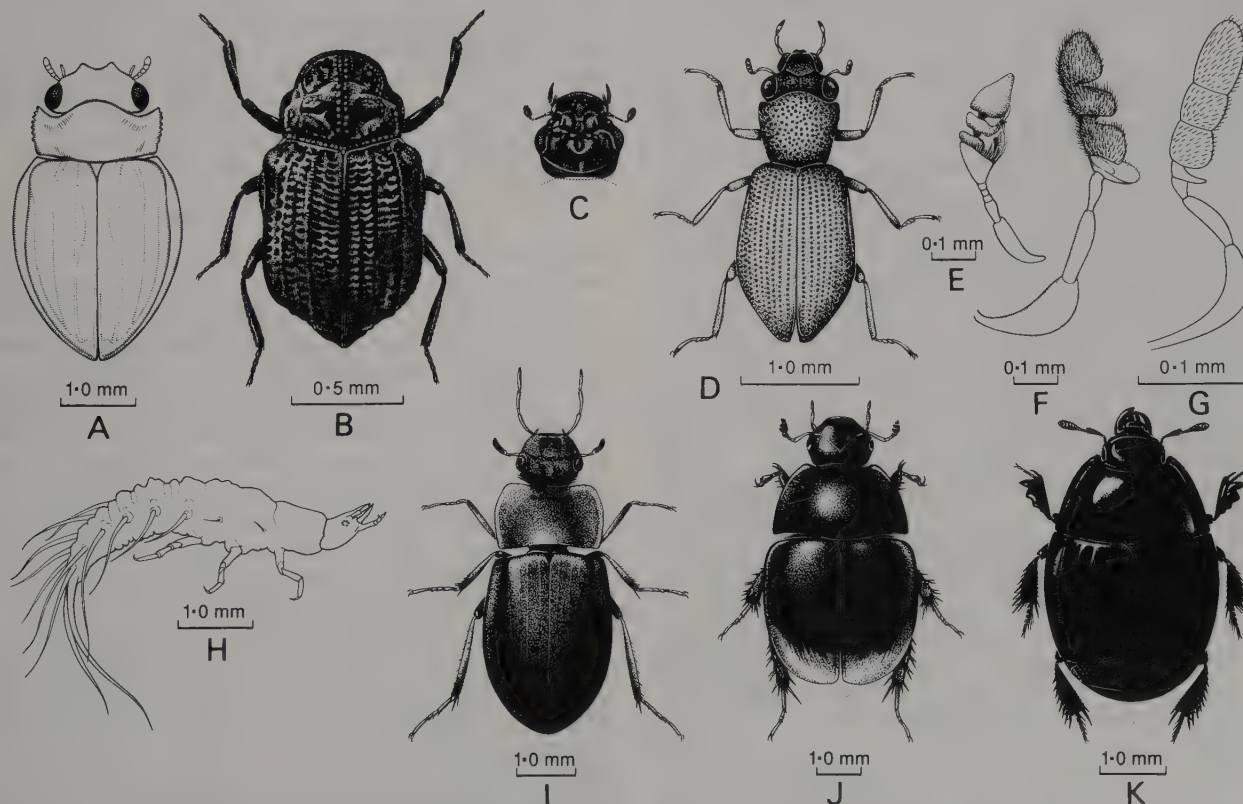


Fig. 35.23 A–J, Hydrophilidae: A, *Spercheus platycephalus*, Spercheinae; B, *Georissus australis*, Georissinae; C, same, head; D, *Hydrochus serricollis*, Hydrochinae; E, *Hydrophilus* sp., Hydrophilinae, antenna; F, *Berosus australis*, Berosinae, antenna; G, *Hydrochus* sp., Hydrochinae, antenna; H, *Berosus* sp., larva; I, *Helochaeres australis*, Hydrobiinae; J, *Sphaeridium discolor*, Sphaeridiinae; K, *Hister walkeri*, Histeridae. [F. Nanninga]

35.23E–G), the large clypeus and more or less angulate frontoclypeal suture, often attached to a median line (endocarina), and the well-developed maxillary palps, which are usually longer than the antennae. Larvae vary somewhat in form, but are typical for the superfamily, except for the presence of a maxillary mala in *Spercheus*. They differ from histerid larvae by having 6 stemmata on each side and usually possessing a metapneustic respiratory system, with only the 8th spiracles functional and these located in a respiratory chamber (atrium) at the end of the abdomen. Adult and larval hydrophilids have very different habits, although occupying the same habitats; the former are phytophagous or saprophagous, while the latter are predacious (except in a few exotic *Helophorus*).

*Spercheus platycephalus* (Fig. 35.23A) (SPERCHEINAE) is a brown beetle with coarsely punctate and costate elytra and a pubescent cupule; larvae differ from those of most hydrophilids in having an apical lobe (mala) on the maxilla and reduced spiracles. Spercheines inhabit stagnant ponds and adults and larvae are reported to walk on the underside of the surface film. *Georissus* (Figs 35.23B, C) (GEORISSINAE) is minute, black and tuberculate, with a deflexed head concealed from above, a compact 1- or 3-segmented antennal club, large fore coxae fused to their trochanters, and 2 connate ventrites; larvae are typical for the family but lack a respiratory chamber and have 8 pairs of laterally placed spiracles. *Hydrochus* (HYDROCHINAE) (Fig. 35.23D) resembles hydraenids in being elongate, narrow and somewhat metallic; it is found attached to plants in ponds or slow-moving creeks. The related Epimetopinae and Helophorinae do not occur in Australia.

The remaining groups of Hydrophilidae include the mainly terrestrial SPHAERIDIINAE and the aquatic BERSINAE, AMPHIOPINAE, CHAETARTHRIINAE, HYDROBIINAE and HYDROPHILINAE. The sphaeridiines are small to minute and may be abundant in decaying vegetable matter, dung, carrion and damp soil. The introduced *Cercyon haemorrhoidalis* and *Sphaeridium discolor* (Fig. 35.23I) are common dung inhabitants; species of the endemic genus *Notocercyon* may be abundant in forest litter; and *Pseudohydrobius* species may be found in flowers (especially of *Leptospermum*). Most aquatic hydrophilids are oval to globose, smooth and glabrous, often resembling Dytiscidae, from which they differ in having short, clubbed antennae and long maxillary palps. A ventral plastron, which communicates with the subelytral air reservoir, is also present; when the beetle rises to the surface, it breaks the surface film using its specialised antennal club, allowing communication between atmosphere and plastron. Larvae of Bersinae (Fig. 35.23H) are unique in lacking functional spiracles (apneustic) and in having 7 pairs of lateral gills. The largest Australian species belong to *Hydrophilus*. [J. M. E. Anderson 1976; van Emden 1956; Watts 1987, 1988b]

**12. Histeridae** (Fig. 35.23K). ADULT: ANT 8–11(1/3), FCOX TRANS(CONC), FCAV OPEN(OPEN), MCOX VWIDE(OPEN), 5-5-5/5-5-4, ABD 5(0), 1–16 (1.3–12) mm. LARVA: HEAD PRO(PRO), STEM 0/1, ANT 3, FSUT 0, LABR FU, MOLA 0, VMP PRO, MALA 0,

MP 4/5, LP 2/3, HSC 0, HRD 0, VER 0, LEGS 5, TS 0/2, UROG 0R/+, SPIR BI.

Although adults vary considerably in shape, histerids are relatively easy to recognise by their compact form, deeply inserted head, large, transverse fore coxae, dentate fore tibiae, antennae which are almost always geniculate and have a compact, pilose club, and elytra which have 6 or fewer striae and are truncate, exposing 1 or 2 abdominal tergites. Most are black, glabrous and shiny, but some *Saprinus* are metallic green, CHLAMYDOPSINAE are often red and may have erect setae or setal tufts, and *Epiechinus* are clothed with scale-like setae. The body is usually oblong to ovoid or globose, but some histerids (*Trypeticus*, *Niponius*) are elongate and cylindrical, while others (*Hololepta*, *Platysoma*) are strongly flattened. Larvae resemble those of Hydrophilidae in general form and head structure, but they have a full set of functional, biforous spiracles, a penicillus of hairs at the base of each mandible, and (almost always) 2-segmented urogomphi, and they lack an apical respiratory chamber and have either no stemmata or only 1 pair.

Both adults and larvae are carnivorous, feeding mainly on the larvae of other insects. They are commonly found in carrion, dung and decaying vegetable matter or under bark of dying or dead trees, where they usually prey on fly larvae. Some species (in Teretriini, Trypeticini and NIPONIINAE) inhabit the burrows of wood-boring insects, such as Bostrichidae and scolytine weevils; some Saprinini and Histerini may be found in carrion and dung; *Hypocaccus*, *Halacritus* and some *Saprinus* are common in beach drift; and *Hololepta* and *Platysoma* occur under bark. The myrmecophilous chlamydopsines have setose secretory structures (trichomes) which apparently produce an appeasement substance (Wilson 1971) necessary for their acceptance within ant colonies. [Froggatt 1927; J. C. M. Gardner 1930; Hinton 1945b; Mazur 1984]

### Superfamily STAPHYLINOIDEA

Adults variable but characterised by reduced hind wing venation without R-M loop, aedeagus with phallobase reduced or absent, and 4 free Malpighian tubules. Procoxae usually strongly projecting, metasternum almost always lacking median suture or line, legs often spinose with simple tarsi (at least on hind legs), 2nd abdominal sternite usually visible only laterally, elytra often truncate, exposing 1 to several tergites. In larvae, galea and lacinia closely associated or fused to form mala, mandibles often without mola, 2nd antennal segment apically oblique and with sensorium attached basad of segment 3, segment 9 usually with pair of articulated urogomphi, spiracles usually annular with closing apparatus.

Two recent and substantially different views on staphylinoid phylogeny and classification have been published by Lawrence and Newton (1982) and Naomi (1985); the latter suggested formal changes in classification, which have been criticised by Newton and Thayer (1988). The system used here is more or less that of Britton (1970), except for the inclusion of Hydraenidae and the submerging of Limulodidae and Scaphidiidae into Ptiliidae and Staphylinidae, respectively.



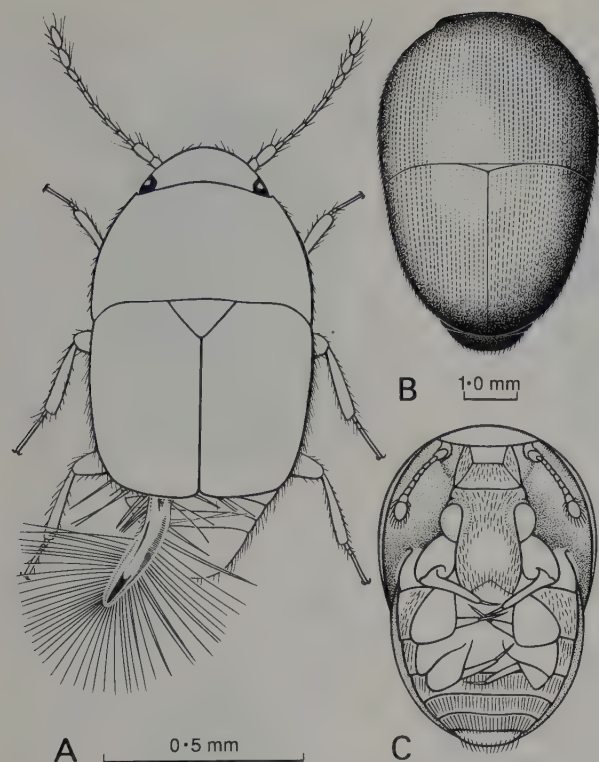


Fig. 35.24 Ptiliidae: A, *Acrotrichis* sp., with part of one hind wing exposed; B, *Rodwayia orientalis*, dorsal; C, same, ventral.

[A by A. Hastings; B, C by F. Nanninga]

**13. Hydraenidae** (Limnebiidae; Figs 35.25A, B). ADULT: ANT 8R–9(5–6R), FCOX TRANS–GLOB (EXP), FCAV OPEN–CLOS(OPEN–CLOS), MCOX NARR–MWIDE(OPEN), 5-5-5/4-4-4A, ABD 6–7(0), 0.8–2.6 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT +, LABR FR, MOLA +, VMP RET, GLAC/MALA, MP 3, LP 2, HSC 0/+, HRD 0, VER 0, LEGS 5, TS 2, UROG +, SPIR AN.

Small beetles with relatively inconspicuous antennae, often concealed within grooves beneath head and cavities between prosternum and pronotal hypomera, and well-developed maxillary palps, which may be as long as or longer than antennae. The segment preceding the antennal club usually forms a cupule like that in Hydrophilidae, but this is not always the case and sometimes it is the pedicel which is cupule-like. Larvae usually elongate and campodeiform, with well-developed legs, articulated urogomphi, and a pair of hooks on segment 10, but those of *Tympanogaster* species are more flattened, with paired lateral thoracic and abdominal plates and a pair of spiracular tubes projecting dorsally from between prothorax and mesothorax. Hydraenids feed on algae in a variety of aquatic, riparian and littoral habitats, including streams, waterfalls, wet rock faces, ponds and ditches, marine rock pools, seabird nests, and inland salt lakes. Most adults are capable of breathing in water by means of a plastron formed by hydrofuge hairs on their ventral surfaces, but most larvae have no aquatic modifications. Exceptions occur in the genus *Tympanogaster*, where both larvae and adults live in the splash zone beneath waterfalls and lar-

vae breathe through the spiracular tubes mentioned above. *Hughleechia giulianii* is a marine intertidal species, living in rock crevices and pools within the high tide splash zone. The family is represented in Australia by two genera of HYDRAENINAE (*Hydraena* and *Limnebius*) and five described genera of OCHTHEBIINAE (*Ochthebius*, *Gymnochthebius*, *Tympanogaster*, *Hughleechia* and *Meropathus*). [Newton 1985; Perkins 1980, 1981; Zwick 1977a]

**14. Ptiliidae** (incl. Limulodidae; Fig. 35.24). ADULT: ANT 10–11(2–3), FCOX TRANS–GLOB (EXP/CONC), FCAV OPEN(OPEN/CLOS), MCOX NARR–MWIDE (CLOS), 2-2-2/3-3-3R, ABD 6–7(0), 0.4–1.1 mm. LARVA: HEAD HYPO, STEM 0, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, GLAC/MALA, MP 3, LP 2, HSC 0/+, HRD 0, VER 0, LEGS 5, TS 2, UROG 0R/+, SPIR AN.

Minute beetles with filamentous antennae clothed with whorls of long hairs and narrow hind wings fringed with very long hairs (Fig. 35.24A). Body usually somewhat flattened and pubescent; elytra entire or truncate, exposing 1–3 abdominal tergites; tarsi almost always 2-segmented and may appear to be 1-segmented. Hind coxae transverse and contiguous to oval and widely separated, and coxal plates strongly developed to absent. Species of *Cochliarion* and species of *Rodwayia* (Figs 35.24B, C) differ from other Australian ptiliids in having the body more convex and compact, the hind wings and eyes absent, the head more deflexed and the antennae shorter. Larvae elongate and lightly sclerotised, with short, articulated urogomphi (rarely absent); pupa obtect.

Ptiliidae are relatively abundant in decaying organic matter, including leaf litter, compost heaps, rotten logs, tree holes and dung, where their major food source appears to be fungal spores and hyphae. Some species live within the pore tubes of bracket fungi (Polyporaceae), where they feed on developing spores. *Actinopteryx fucicola* occurs in decaying seaweed on sea coasts throughout the world. Species of *Rodwayia* occur in the nests of ants; they are largely ignored by their hosts and appear to feed on larval exudations. [Dybas 1976; Seevers and Dybas 1943]

**15. Leioididae** (Anisotomidae, Catopidae, Cholevidae; Figs 35.25C, D). ADULT: ANT 10–11(3–5), FCOX GLOB–PROJ(EXP), FCAV OPEN(OPEN/CLOS), MCOX CONT–MWIDE(OPEN), 5-5-5/5-5-4/5-4-4/4-4-4/3-3-3, ABD 4R/5R/6(0), 1.2–5 mm. LARVA: HEAD PRO(PRO), STEM 1–3/5, ANT 3, FSUT 0, LABR FR, MOLA 0/+, VMP RET, GLAC/MALA, MP 3, LP 2, HSC 0/+, HRD 0, VER 0, LEGS 5, TS 2, UROG +, SPIR AN/AB.

Moderately small beetles with more or less spiny legs and simple tarsi (fore and occasionally mid tarsi modified in some males and in *Colon*), differing from most other staphylinoids in having the abdomen entirely concealed by the elytra. Almost all species with 5-segmented antennal club, having 2nd segment (8) smaller (shorter or shorter and narrower) than either 1st (7) or 3rd (9); club sometimes very weak (*Eublackburniella*, Fig. 35.25C; *Nargiotes*) with segment 8 only slightly reduced, or very

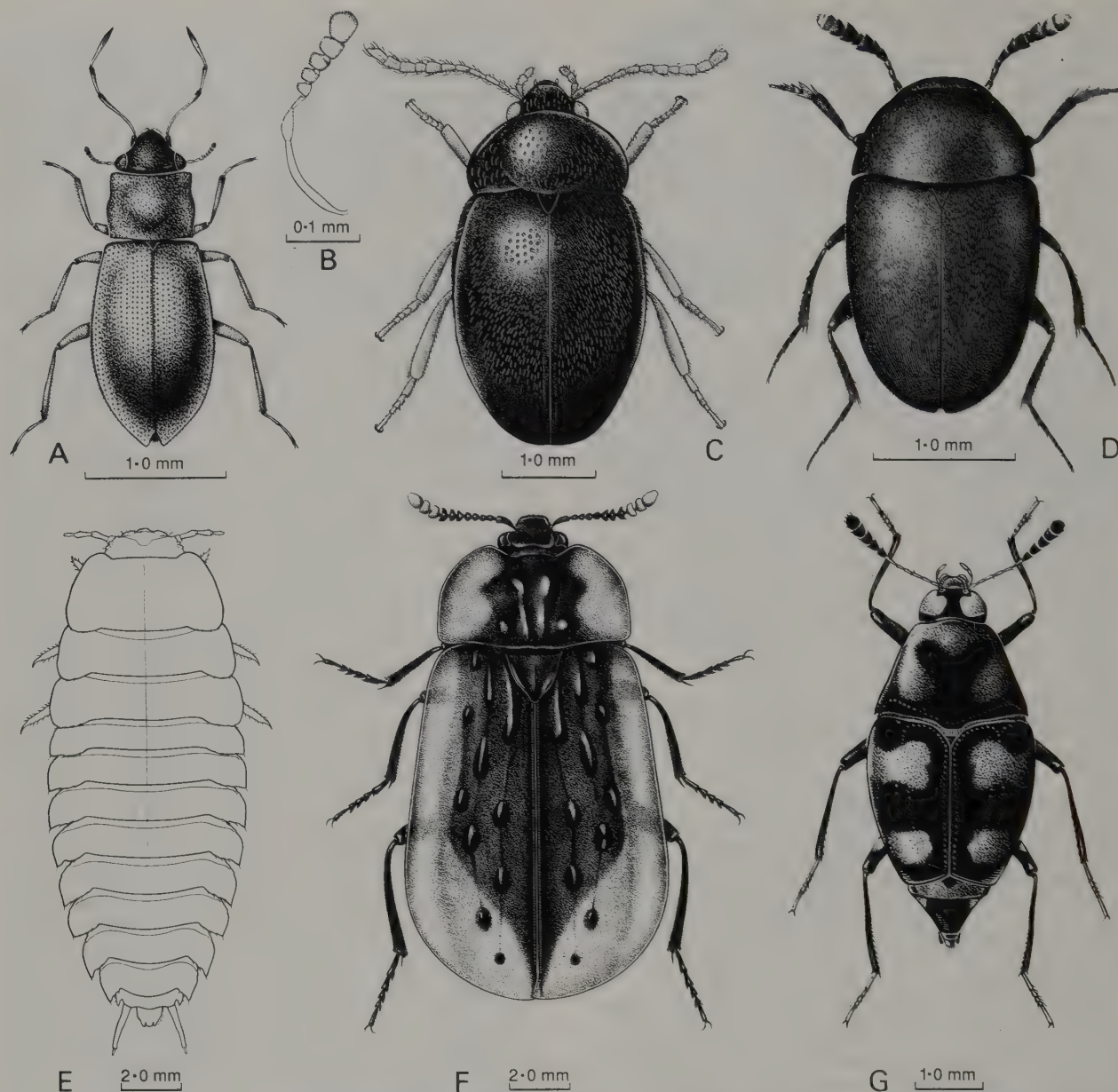


Fig. 35.25 Staphylinoida: A, *Hydraena luridipennis*, Hydraenidae; B, *Ochthebius* sp., Hydraenidae, antenna; C, *Eublackburniella* sp., Leiodidae-Camiarinae; D, *Pseudonemadus australis*, Leiodidae-Cholevinae; E, *Ptomaphila lacrymosa*, Silphidae, larva; F, same, adult; G, *Scaphidium punctipenne*, Staphylinidae-Scaphidiinae.

[A, B, D, F, G by F. Nanninga; C by A. Hastings; E by A. Klinkenberg]

strong (*Dietta*, *Zeadolopus*) with 8 greatly reduced or absent. *Colon* differs in having a 4-segmented club with segment 8 larger than 7. Leiodids also possess a unique type of internal sensory vesicle usually opening on the distal surfaces of segments 7, 9 and 10 (Corbière-Tichané 1974; Peck 1977). Larvae, like those of most staphylinoids, are of the active, campodeiform type with urogomphi which are almost always articulated at the base; they differ from staphylinid larvae in usually having mandibular mola and 2 apical maxillary lobes (galea and lacinia).

Leiodidae are abundant in decaying organic matter and also occur in carrion, fungus fruiting bodies, some types of dung and nests of vertebrates; they are abundant in caves in most parts of the world but have not yet been

recorded from Australian caves. Many are general scavengers, but certain groups are associated with particular fungi (*Neopelatops* with slime moulds; some *Nargomorphus* with puffballs; some leiodines and probably *Colon* with hypogean fungi) (Newton 1984). Species of *Myrmecholeva* are very unusual in that both larvae and adults have suctorial mouth-parts consisting of a labrolabial tube and styliferous mandibles and maxillae; they have been recorded from ant nests (Lea 1910a) but appear to be more generally distributed and may be mycophagous, rather than predacious.

LEIODINAE are usually glabrous and strongly convex and may have burrowing adaptations, such as enlarged legs (*Dietta*, *Zeadolopus*); most other leiodids are



pubescent. CAMIARINAE, including *Eublackburniella*, *Myrmecholeva* and the Agyrtonini, are restricted to the Southern Hemisphere, while the CHOLEVINAE occur throughout the world and are represented in Australia by *Austronemadus*, *Catoposchema*, *Nargiotes* and several other genera. COLONINAE (*Colon*) also occur in Australia, but Catopocerinae and Leptininae are absent from the fauna. [Newton 1985; Zwick 1979b]

**16. Scydmaenidae** (Fig. 35.26A). ADULT: ANT 11(INC/3-5), FCOX TRANS-PROJ(CONC), FCAV OPEN(OPEN), MCOX NARR(CLOS), 5-5-5, ABD 6(0), 0.8-2.9 mm. LARVA: HEAD PRO(PRO)/HYPO, STEM 0/1/3, ANT 2/3, FSUT 0, LABR FU, MOLA 0, VMP RET, MALA, MP 2/3, LP 2, HSC 0, HRD 0, VER 0, LEGS 5, TS 2, UROG 0/+R, SPIR AN.

Small to minute beetles usually distinguished by their 'waisted' body form, with distinct constriction at junction of prothorax and elytra and usually another at base of head, so that neck is formed. Most species reddish and pubescent, with coarsely faceted eyes, large maxillary palps with reduced apical segment, approximate fore coxae and distant hind coxae, no lateral pronotal carinae and clavate femora. Species of Cephenniini are exceptional in lacking the neck and waist, but in most respects they are typical scydmaenids. Larvae elongate to ovate and setose, with large, club-like antennae and usually without or with very small urogomphi.

Scydmaenids occur in a variety of habitats, such as leaf litter, rotten wood, moss, tree holes, sawdust piles and ant nests. They are considered to be predators, and at least one cephenniine larva was observed feeding on oribatid mites, which it captured with the aid of an adhesive device (Schuster 1966) probably consisting of labial discs, such as those described by Newton (1991). The family is represented in Australia by four tribes of the subfamily SCYDMAENINAE: Cephenniini (*Coatesia*, *Neseuthia*), Syndicini (*Syndicus*), Scydmaenini (*Scydmaenus*, *Palaeoscydmaenus*), and Euconnini (several genera including *Euconnus*, *Horaemorphus* and *Stenichnus*). [Franz 1975]

**17. Silphidae** (Figs 35.25E, F). ADULT: ANT 11(3), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX MWIDE(OPEN), 5-5-5, ABD 7(0), 14-42 mm. LARVA: HEAD HYPO, STEM 6, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP RET, GLAC, MP 3, LP 2, HSC 0, HRD +, VER +, LEGS 5, TS 2, UROG +, SPIR AN.

Relatively large and flattened beetles with a distinctive antenna (large, 3-segmented, slightly asymmetrical and finely pilose club preceded by at least one glabrous, strongly transverse, concave segment reminiscent of hydrophilid cupule, Fig. 35.25F, cf. Fig. 35.23F); unlike Hydrophilidae, silphids have relatively long, 11-segmented antennae. Body either glabrous or clothed with very short, fine hairs; eyes moderately large and protuberant; fore coxae large and projecting, all tarsal segments clothed beneath with yellow hairs. In *Ptomaphila* the elytra are provided with short, longitudinal ridges and tubercles and completely conceal the abdomen, while in *Diamesus* they are carinate and truncate, exposing 4 or 5 abdominal tergites. Larvae (Fig. 35.25E) broad,

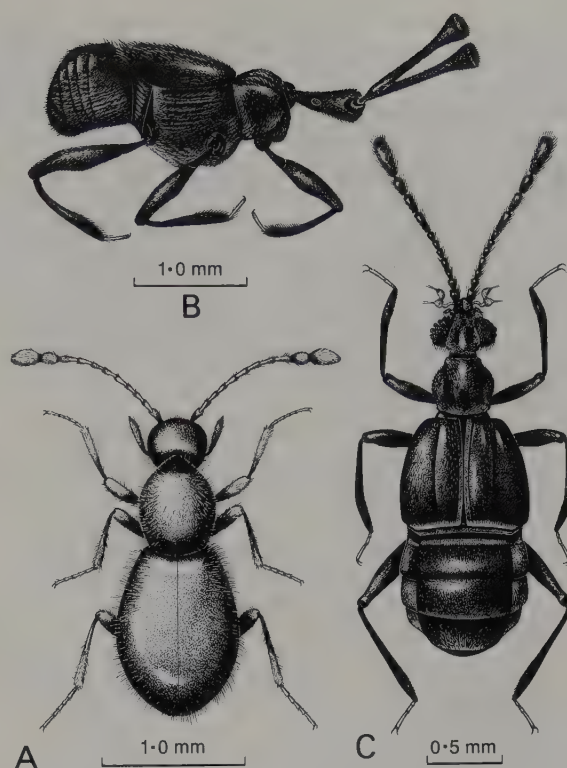


Fig. 35.26 Staphylinidae: A, *Scydmaenus myrmecophilus*, Scydmaenidae; B, *Tiracerus foveicollis*, Pselaphidae; C, *Ctenicellus major*, Pselaphidae. [F. Nanninga]

depressed, and heavily sclerotised, with lateral, plate-like expansions on thorax and abdomen.

Australian Silphidae are associated with vertebrate carcasses, but *Ptomaphila lacrymosa* adults have also been observed feeding on maggots; in other parts of the world there are phytophagous forms, as well as carrion feeders and those which prey on snails. *Diamesus osculans* is widely distributed from India and Indonesia, through Papua New Guinea to northern and eastern Australia; *P. lacrymosa* occurs in the south-eastern and south-western part of the continent; and *P. perlata* is confined to the eastern coast from East Gippsland to Cape York. *Oxelytrum*, the apparent sister group of *Ptomaphila*, occurs in Central and South America. [Peck and Anderson 1985; O. P. Young 1983]

**18. Staphylinidae** (incl. Scaphidiidae; Figs 35.25G, 27A-G; Plate 5, J). ADULT: ANT 10-11(FIL/INC/2-6), FCOX TRANS-PROJ(EXP/CONC), FCAV OPEN-CLOS(OPEN-CLOS), MCOX CONT-MWIDE (OPEN-CLOS), 5-5-5/4-5-5/4-4-4/4-4-5/5-5-4R/3-3-3, ABD 6-7(0), 1-20 mm. LARVA: HEAD PRO(PRO), STEM 0-6, ANT 3/4, FSUT 0, LABR FR/FU, MOLA 0, VMP RET/PRO, MALA, MP 3/4, LP 2/3, HSC 0, HRD 0, VER 0/+, LEGS 5, TS 0-M, UROG 0R/+, SPIR AN.

This is the 5th largest family in Australia, and many species remain to be discovered. Adults usually more or less elongate with truncate elytra that nearly always leave more than half the abdomen exposed; all but first 1 or 2 tergites heavily sclerotised and often flanked by paratergites; abdominal intersegmental membranes usually with

pattern of minute sclerites. Larvae always without mandibular mola and usually with articulated urogomphi. In three of the largest subfamilies (Aleocharinae, Paederinae and Staphylininae) the body is rather loosely organised and flexible, and the prothorax has strongly projecting coxae, reduced notal projections, and much exposed membrane (Fig. 35.27c). Staphylinid larvae are usually of the active, campodeiform type with well-developed legs, characteristic antennae in which the apex of segment 2 is oblique so that the sensorium arises before the apex, and a pair of articulated urogomphi on T9. A few forms are onisciform, however, and some may have fixed or no urogomphi.

*Key to the Subfamilies of Staphylinidae Known in Australia*

1. Antennal insertions located posterior to a line drawn between anterior edges of eyes ..... 2
- Antennal insertions located anterior to a line drawn between anterior edges of eyes ..... 4
- 2(1). Elytra concealing all but last 1 or 2 abdominal tergites; body short, stout and wedge-shaped, with long and slender legs and antennae ..... SCAPHIDIINAE
- Elytra exposing at least 3 abdominal tergites; body not wedge-shaped ..... 3
- 3(2). Hind coxae oval and distinctly separated; eyes large and protruding, so that head is wider than prothorax ..... STENINAE
- Hind coxae strongly transverse and contiguous; eyes not large and protruding ..... ALEOCHARINAE
- 4(1). Head with paired ocelli, about level with the posterior edges of the eyes, or if ocelli indistinct, then elytra concealing all or all but 1 or 2 tergites and antennae with distinct 3-segmented club ..... OMALIINAE
- Head without paired ocelli; without other characters in combination ..... 5
- 5(4). Antennae with distinct 2-segmented club ..... 6
- Antennae without distinct club ..... 7
- 6(5). Eyes very large and protuberant; labrum deeply emarginate and partly concealed, so that only a pair of narrow, setose processes are visible; length more than 2.5 mm ..... MEGALOPSIDINAE
- Eyes not very large and protuberant; labrum not as above; length usually less than 2.5 mm ..... EUAESTHETINAE
- 7(5). Apical segment of maxillary palp enlarged and cul-triform, with a groove along one side ..... PAEDERINAE-Pinophilini
- Apical segment of maxillary palp not enlarged, without a groove ..... 8
- 8(7). Abdomen with 7 ventrites (S2–S8) ..... OXYTELINAE (pt)
- Abdomen with 6 ventrites (S3–S8) ..... 9
- 9(8). Antennal insertions concealed from above by paired frontal ridges ..... 10
- Antennal insertions exposed ..... 14
- 10(9). Abdomen without paratergites; usually cylindrical without any sutures or carinae separating tergites and sternites, occasionally with sharp lateral edges in flattened, yellowish forms with basally constricted prothorax ..... OSORIINAE
- Abdomen with paratergites separating the tergites and sternites ..... 11
- 11(10). Fore coxae small and globular; body elongate and narrow, with long, filiform, setose antennae and anteriorly projecting horns on head ..... PIESTINAE
- Fore coxae larger, projecting; head without horns ..... 12
- 12(11). Fore coxae transverse, cavities partly closed behind by triangular spiracular sclerite ..... PROTEININAE (pt)
- Fore coxae projecting, not transverse; without visible spiracular sclerite behind fore coxae ..... 13
- 13(12). Apical segment of maxillary palp much longer than preceding segment ..... OXYTELINAE (pt)
- Apical segment of maxillary palp reduced, much shorter than preceding segment ..... PAEDERINAE (pt)
- 14(9). Tarsi 3-segmented; minute (less than 1.5 mm), extremely slender, wingless and eyeless ..... LEPTOTYPHILINAE
- Tarsi with more than 3 segments; size larger or not very slender ..... 15
- 15(14). Elytra long, leaving only 3 or 4 abdominal tergites exposed, and hind coxae with vertical posterior face ..... PROTEININAE (pt)
- Elytra shorter, or if long, hind coxae with oblique posterior face visible from below ..... 16
- 16(15). Head without distinct neck visible from above (head more or less deeply inserted into prothorax) ... 17
- Head with distinct neck visible from above ..... 18
- 17(16). Elytral epipleuron not separated by a carina ..... PHLOEOCHARINAE
- Elytral epipleuron separated by a carina ..... TACHYPORINAE
- 18(16). Pronotum with distinct, post-coxal projection, usually concealing mesothoracic spiracle in lateral view; abdominal intersegmental membranes with brick-like pattern of minute rectangular sclerites; apical segment of maxillary palp always reduced, much shorter than preceding segment ..... PAEDERINAE (pt)
- Pronotum without post-coxal process; abdominal intersegmental membranes with pattern of minute triangular or rounded sclerites; apical segment of maxillary palp variable, usually longer than preceding segment ..... STAPHYLININAE

The OMALIINAE and PROTEININAE include a number of small and usually flattened species occurring in the southern part of the continent and having affinities with the New Zealand and South American faunas (Newton 1985; Thayer and Newton 1978). In two unusual omaliine genera, *Glypholoma* and *Microsilpha*, the elytra are nearly complete. TACHYPORINAE are a moderately sized group with a characteristic fusiform shape, inserted head, and tapered abdomen with the segments capable of being telescoped. A common genus is *Sepedophilus*; some species graze on the undersides of bracket fungi. ALEOCHARINAE are the largest group of staphylinids, with more than 200 described Australian species and many more awaiting study. The vast majority of aleocharines are free-living predators, but *Aleochara* species are ectoparasitoids of



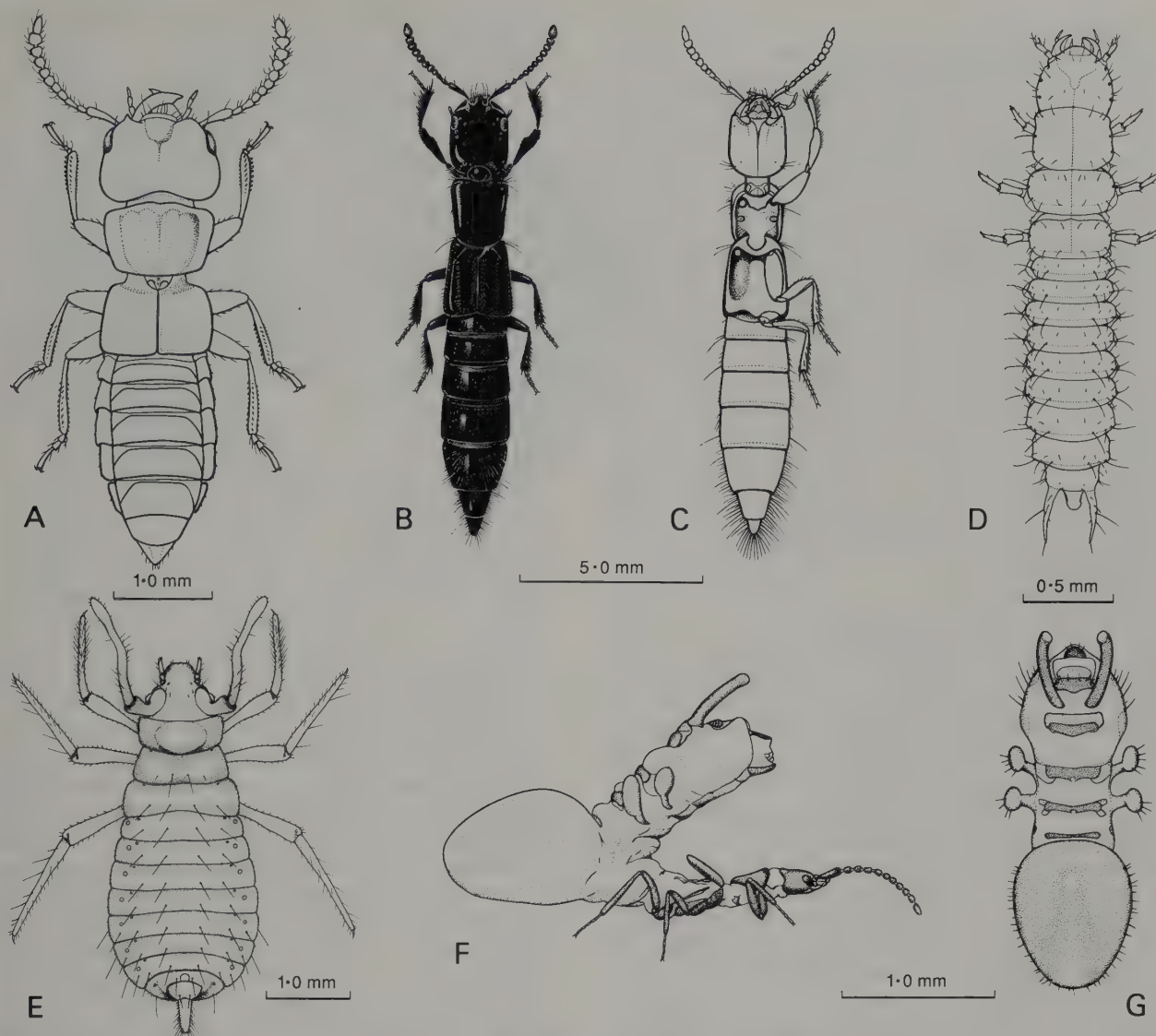


Fig. 35.27 Staphylinidae: A, *Anotylus* sp., Oxytelinae; B, *Thyrecephalus chalcopertus*, Staphylininae, dorsal; C, same, ventral; D, *Omalius* sp., Omaliinae, larva; E, *Drepanoxenus ardea*, Aleocharinae, adult; F, *Austrospirachtha mimetes*, Aleocharinae, adult, lateral; G, same, dorsal.

[A by A. Hastings; B, C by F. Nanninga; D by A. Klinkenberg; E by R. Kohout; F, G by B. Rankin]

Diptera pupae (Drea 1966) and *Gyrophana* and their relatives feed on Basidiomycetes (Ashe 1984). Inquilinism has evolved a number of times in aleocharines. In Australia, *Polylobus* and many Myrmedoniini occur with ants, while seven tribes (including Coroticini, Drepanoxenini and Trichopseniini) and three subtribes of Athetini are composed of termitophiles (Kistner 1979, 1982; Watson and Kistner 1985; Watson and Howick 1975).

The SCAPHIDIINAE are often considered to be a separate family because of the distinctive wedge-like form and relatively long elytra. Most scaphidiids feed on the spores and hyphae of various Basidiomycetes, but species of *Baeocera* and *Scaphobaeocera* are slime mould spore feeders. A common genus associated with polypores is *Scaphisoma*. PIESTINAE are represented by *Prognathoides mjobergi*, a distinctive flattened staphylinid with paired horns on the head. OSORIINAE are primarily tropical, saprophagous and found under bark and in rotten wood.

Included are the large, flattened *Priochirus miles* from North Qld, cylindrical species of *Osorius*, and the very small, flattened Eleusinini. *Thoracophorus* are thought to be mycetophagous. OXYTELINAE are primarily saprophagous and some are abundant in leaf litter and dung; our commonest genus is *Anotylus*. The flightless, litter-inhabiting *Oxyptus peckorum*, from south-western W.A., is a relict form most closely related to species of *Euphanias* from the Mediterranean Region and South America (Newton 1982). *Sartallus signatus* occurs under seaweed on beaches, and species of *Bledius* construct burrows in moist sand adjacent to rivers, lakes and oceans and feed on algae and diatoms (Herman 1986). *Stenus* (STENINAE) live in marshes and at the edges of streams, where they are able to move on the surface of water by secreting from the pygidial glands a surfactant, which reduces the surface tension behind them (Schildknecht 1970; Schildknecht *et al.* 1975). *Stenus* also possesses a

unique adult prey capture mechanism, consisting of a protrusible, adhesive labium (Weinreich 1968).

PAEDERINAE and STAPHYLININAE are the two largest groups of highly motile, specialised predators. *Paederus* (Plate 5, J) is well known, brightly coloured and, when irritated, produces a fluid that causes severe blistering of the skin (Frank and Kanamitsu 1987; Whelan and Weir 1987). Other common genera are *Lathrobium*, *Scopaeus*, *Hyperomma* and *Pinophilus*. Among the staphylinines, *Creophilus erythrocephalus*, the devil's coach-horse, which is black with a red head bearing a central black spot, is often associated with cadavers, where it preys on maggots. Large and metallic species of *Actinus* occur in North Qld, while *Cafius* are predators in seaweed on beaches. Other major groups are the genera *Philonthus*, *Quedius*, *Heterothops* and the tribe Xantholinini. *Myotyphlus jansoni* lives in the fur of native *Rattus* and may be related to South American species with similar habits (Hamilton-Smith and Adams 1966). [Frank and Thomas 1984; Kasule 1966; Moore and Legner 1979; Newton 1984]

**19. Pselaphidae** (Figs 35.26B, C). ADULT: ANT 2–11 (FIL/INC/2–5), FCOX PROJ(CONC), FCAV OPEN (OPEN), MCOX CONT–NARR, 3–3–3/2–2–2<sub>R</sub>, ABD 6(0), 0.8–3.6 mm. LARVA: HEAD PRO(PRO), STEM 0/2/3, ANT 2/3, FSUT 0, LABR FU, MOLA 0, VMP RET, MALA, MP 3, LP 2, HSC 0, HRD 0, VER 0/+, LEGS 5, TS 0/2, UROG 0/+, SPIR AN.

Small beetles resembling Staphylinidae in having short, truncate elytra exposing most of abdomen, but differing from staphylinids in having shorter, broader and non-flexible abdomen, enlarged apical maxillary palp segment, setose foveae on head, prothorax and other parts of body, and 2- or 3-segmented tarsi usually with unequal claws or 1 claw only. The colour is usually reddish or yellowish, and the antennae are almost always incrassate or variously clubbed. Larvae elongate to fusiform and clothed with erect setae; antennal sensorium enlarged or complex; paired eversible glands arising from antennal sockets; urogomphi reduced and fixed or absent. Pselaphidae are abundant in leaf litter, rotten wood, moss, tree holes, caves and animal nests; except for some myrmecophilous forms, adults and larvae are predators on minute organisms. The European *Batrises oculatus* was observed feeding on a collembolan, which it captured by sticking the prey to its abdomen, which was covered with a viscous substance secreted by dorsal glands (De Marzo 1986); the same species formed a silken cocoon for pupation.

The family is well represented in Australia by members of all recognised subfamilies: FARONINAE with the genus *Sagola*, EUPLECTINAE and BATRISINAE with about 80 described species between them, GONIACERINAE and PSELAPHINAE, the most diverse and abundant groups together comprising over 300 species, and CLAVIGERINAE, represented mainly by about 50 species of *Tiracerus*. The last are highly specialised myrmecophiles which are tolerated in ant nests and even fed by workers; they bear setose secretory structures (trichomes), which in an American species, *Adranes taylora*, are fed upon by larvae

of the ant *Lasius niger* (Akre and Hill 1973). [Newton and Chandler 1989; Besuchet 1956b]

## Series EUCINETIFORMIA Superfamily EUCINETOIDEA

The three families Scirtidae, Eucinetidae and Clambidae retain many primitive polyphagan features but share a type of compacting mechanism in which the head is strongly hypognathous and fits against the fore coxae or metasternum (Clambidae) when at rest. Larvae of Clambidae and Eucinetidae are similar to those of many Cucujoidea, usually differing in the presence of a distinct galea and lacinia and annular spiracles. Scirtid larvae are of a unique type reminiscent of the immature stages of some exopterygote insects, with multiannulate antennae, complex, filter-feeding mouth-parts and a metapneustic respiratory system.

**20. Scirtidae** (Helodidae, Cyphonidae; Figs 35.28B, C). ADULT: ANT 11(FIL), FCOX TRANS–PROJ(EXP), FCAV OPEN(OPEN), MCOX CONT(OPEN), 5–5–5, ABD 5(0–2), 1.5–11 mm. LARVA: HEAD PRO(PRO), STEM 1–3, ANT M, FSUT 0, LABR FR, MOLA +, VMP RET, GLAC, MP 4, LP 2, HSC +, HRD 0, VER 0, LEGS 5, TS 2, UROG 0, SPIR RED.

Moderate to small, oblong to ovoid beetles, usually somewhat flattened, with large, strongly deflexed head, short and broad prothorax with large, projecting fore coxae and reduced sternal region, moderately broad and complete elytral epipleura, and lobed 4th tarsal segments. A pair of sharp genal ridges (Fig. 35.15G) rest against the fore coxae when head is fully deflexed. Hind coxal plates present except in *Scirtes*, which has enlarged hind femora for jumping. Male genitalia are complex and variable within the family (Nyholm 1972). Larvae elongate and somewhat flattened, with large head, multisegmented antennae (unique in beetle larvae), complex mouth-parts with maxillary comb-hairs and comb-like hypopharyngeal armature, a single pair of large spiracles at abdominal apex and a set of 5 anal papillae. Adult scirtids are often found on vegetation near water, while the larvae usually occur in lentic habitats, such as ponds, marshes, bogs or tree holes (Kitching and Allsopp 1987), but have also been found in wet, rotten wood. Larvae are filter-feeding detritivores (Beier 1952). They use the 8th spiracles to breathe at the surface, while the anal papillae are thought to be osmoregulatory in function (Treherne 1954). Scirtids are (e.g. *Macrohelodes*, *Pseudomicrocara*, *Macrocyphon*) most abundant and diverse in the cool temperate parts of Australia. *Scirtes*, which is more common in the north, has enlarged hind femora and is capable of jumping. [Armstrong 1953; Pope 1976]

**21. Eucinetidae** (Fig. 35.28A). ADULT: ANT 11 (FIL/INC), FCOX PROJ(EXP), FCAV OPEN (OPEN), MCOX NARR(CLOS), 5–5–5, ABD 5–7(2), 1.3–3 mm. LARVA: HEAD PRO(PRO)/HYPO, STEM 5, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, GLAC, MP 3, LP 2, HSC +, HRD 0, VER 0, LEGS 5, TS 2, UROG 0, SPIR AN.

Small, fusiform beetles, with reduced prothorax, narrow, deflexed head, very large, oblique hind coxae with



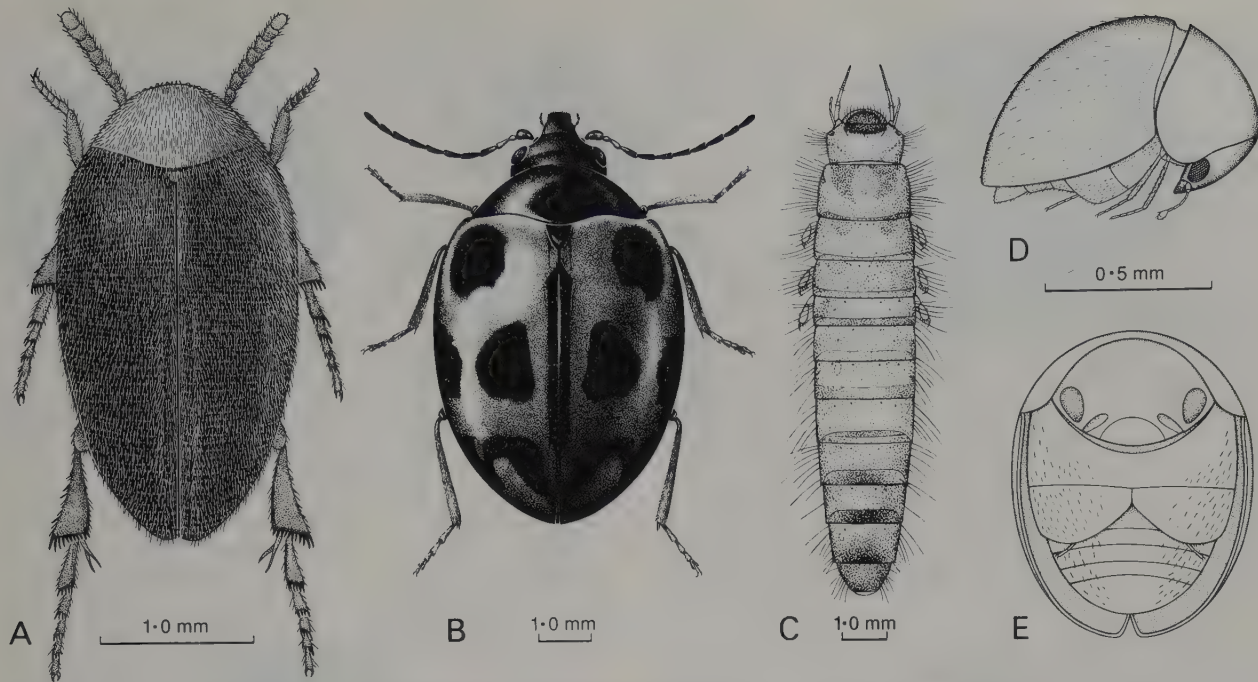


Fig. 35.28 Eucinetoidae: A, *Eucinetus* sp., Eucinetidae; B, *Macrohelodes crassus*, Scirtidae; C, unidentified scirtid larva; D, *Clambus simsoni*, Clambidae, lateral; E, same, ventral. [A by A. Hastings; B–E by F. Nanninga]

plates partly concealing femora, and short legs with mid and hind tibiae and tarsi bearing fringes of dark spines. Larvae more or less oblong and moderately lightly sclerotised with setiferous tubercles dorsally, and broad head narrowed anteriorly. Feeding habits of Australian species are unknown, but some members of the family feed on slime mould spores or the fruiting bodies of Basidiomycetes (Boletaceae, Coniophoraceae) (Wheeler and Hoebeker 1984). Some exotic species have tubular, suctorial mouth-parts (Vít 1977).

**22. Clambidae** (Figs 35.28D, E). ADULT: ANT 10(2), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX CONT–NARR(OPEN), 4–4–4, ABD 5/6(0), 0.9–1.5 mm. LARVA: HEAD PRO(PRO), STEM 0/5/6, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 1/2, HSC +, HRD 0/+, VER 0, LEGS 5, TS 1/2, UROG 0, SPIR AN.

Minute, oval and convex beetles, with partly or entirely divided eyes, and capable of rolling into a ball with head strongly deflexed so that it abuts on metasternum. Hind coxae with large plates which conceal femora. Larvae similar to those of Eucinetidae. Clambids usually occur in leaf litter and haystacks and feed on fungal spores. Australian species belong to the genera *Clambus* and *Sphaerotherax*, but the Palearctic species, *Calyptromerus dubius*, has been accidentally introduced into Tas. [Crowson 1979; Endrödy-Younga 1990]

#### Series SCARABAEIFORMIA Superfamily SCARABAEOIDEA

This is a distinctive group, adults of which are distinguished by: (1) a highly modified, burrowing prothorax, with large coxae (almost always with concealed trochantins and closed cavities) and usually dentate tibiae

with only 1 spur; (2) hind wings with reduced venation and a strong intrinsic spring mechanism for folding; (3) a lamellate antennal club; (4) no hind coxal plates; (5) the 2nd abdominal sternite represented by a lateral portion only; (6) T8 forming a true pygidium and not concealed by T7; and (7) 4 Malpighian tubules. Larvae are grub-like and usually C-shaped, with well-developed antennae and legs, no urogomphi, and usually cribriform spiracles. Trends in the group include the reduction of the 8th abdominal spiracles, movement of the terminal spiracles dorsally or ventrally, loss of the larval spiracular closing apparatus, reduction in the number of adult antennal segments, and increase in the number of larval antennal segments from 3 to 4. The group appears to be primitively adapted for burrowing in soil, with secondary trends in other directions. Loss of the spiracular closing apparatus may have accompanied the development of cribriform spiracles, although in the genus *Trox* the two structures occur together. [Hinton 1967b; Ritcher 1966]

The monophyly of Scarabaeoidea remains undisputed, but the inclusion of Dascilloidea as its sister group within Scarabaeiformia (Crowson 1960) is debatable (see below). Phylogenetic relationships among scarabaeoid families have been discussed by a number of recent authors, including H. F. Howden (1982), Lawrence and Newton (1982), Scholtz (1986a, 1990) and Scholtz *et al.* (1987a,b, 1988). [W. W. K. Houston in press]

**23. Lucanidae** (Fig. 35.29E; Plate 4, N, U). ADULT: ANT 10(3/7), FCOX TRANS–PROJ(CONC), FCAV CLOS(OPEN), MCOX CONT–NARR(OPEN), 5–5–5, ABD 5(0), 6–60 (10–40) mm. LARVA: HEAD HYPO, STEM 0/1, ANT 3/4, FSUT +, LABR FR, MOLA +, VMP RET, GLAC, MP 4, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG 0, SPIR CR.

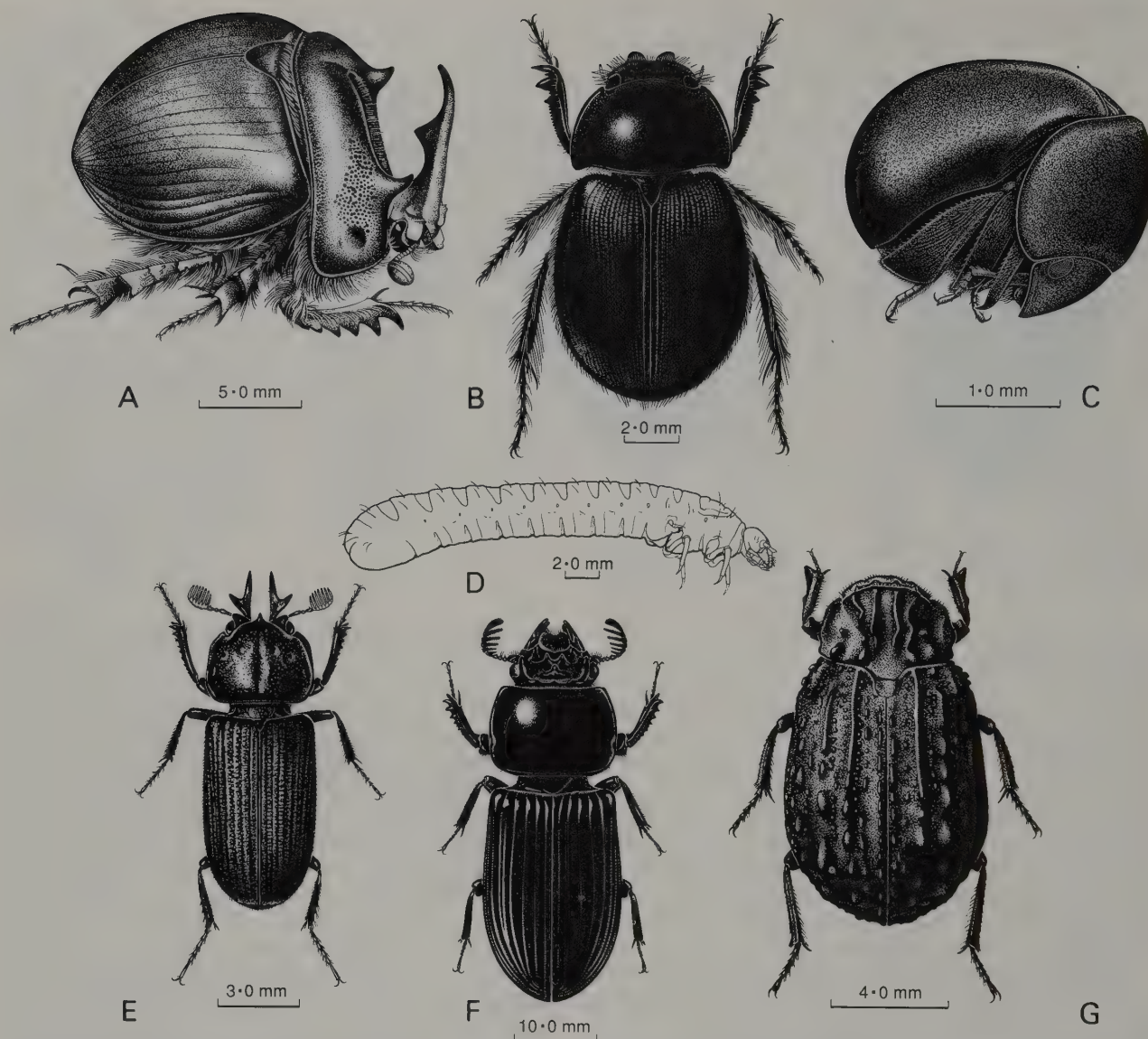


Fig. 35.29 Scarabaeoidea: A, *Blackburnium cavicolle*, Geotrupidae; B, *Phaeochrous emarginatus*, Hybosoridae; C, *Cyphopisthes descarpentriesi*, Ceratocanthidae; D, *Aulacocyclus* sp., Passalidae, larva; E, *Syndesus cornutus*, Lucanidae; F, *Mastachilus quaestionis*, Passalidae; G, *Omorgus australasiae*, Trogidae. [A, B, E–G by F. Nanninga; C by S. P. Kim; D by A. Klinkenberg]

Adults characterised by the relatively thick antennal lamellae, long scape and prognathous head with well-developed mandibles which are often sexually dimorphic; usually black, brown or metallic and usually glabrous but sometimes clothed with scales. Larvae differ from other scarabaeoids in having a stridulatory apparatus consisting of a *pars stridens* on the mid coxa and *pectrum* on the hind trochanter, combined with the lack of transverse folds on the abdominal terga and the presence of a longitudinally oval pad on either side of the vertical anal opening (Lawrence 1981; Ritcher 1966). Adults are mainly nocturnal and some, at least, are nectar feeders, while the larvae feed in rotten wood.

Lucanids are more or less restricted to the wetter parts of the continent. *Syndesus* (SYNDESINAE) differs from most lucanids in having a 7-segmented antennal club with

lamellae longer than usual, while *Ceratognathus* (NICAGINAE) includes smaller species clothed with scales and having 3 long lamellae in the club. The former genus also occurs in New Caledonia and South America, the latter in New Zealand and Argentina. LAMPRIMINAE are represented in Australia by *Lamprima*, *Hololamprima* and *Phalacrognathus*. The magnificent *P. muelleri* (Plate 4, N), the most attractive of Australian beetles, occurs in rainforests of North Qld. *Lamprima* is extremely variable in colour, ranging from metallic green or bronze to blue, red or violet. The remaining genera, all belonging to the LUCANINAE, include *Lissotes*, with many flightless species in Tas., *Sphaenognathus*, whose nearest relatives occur in South America, the endemic *Rhyssonotus*, and tropical *Figulus* and *Prosopocoilus*. [B. A. Holloway 1960; Howden and Lawrence 1974; B. P. Moore 1978, 1984, 1986]



**24. Passalidae** (Figs 35.29D, F). ADULT: ANT 10 (3–6), FCOX TRANS-PROJ(CONC), FCAV CLOS(OPEN), MCOX NARR(CLOS), 5-5-5, ABD 5(0), 18–55. LARVA: HEAD PRO(PRO), STEM 0, ANT 2, FSUT +, LABR FR, MOLA +, VMP RET/PRO, GLAC, MP 3, LP 2, HSC 0, HRD +, VER 0, LEGS 5, TS 2, UROG 0, SPIR CR.

Shining, black, somewhat flattened beetles, with prognathous head, sometimes horned, characteristically curved antennae, and narrow pedicel or waist between prothorax and elytra. Scutellum not visible; elytra conspicuously striate. Adults stridulate by rubbing a plectrum on each hind wing against a pars stridens on the dorsal surface of the abdomen (Reyes-Castillo and Jarman 1983). Larvae differ from those of other scarabaeoids by being less curved and in having the hind leg reduced to a stump, which produces sound when scraped against a file on the mid coxa. Passalids live in rotten logs and exhibit a type of subsocial behaviour discussed in detail by Reyes-Castillo and Halffter (1983). The family is primarily a tropical group, and most Australian species occur in the north. Common Australian genera are *Aulacocyclus*, *Pharochilus* and *Mastachilus*. [Dibb 1938]

**25. Trogidae** (Fig. 35.29G). ADULT: ANT 10(3), FCOX PROJ(CONC), FCAV CLOS(OPEN), MCOX CONT(CLOS), 5-5-5, ABD 5(0), 5.5–30 (7–20) MM. LARVA: HEAD HYPO, STEM 0/1, ANT 3, FSUT +, LABR FR, MOLA +, VMP PRO, GLAC, MP 4, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG 0, SPIR BIR/CR.

Robust, heavily sclerotised, dull and uniformly dark beetles, with tuberculate upper surface, strongly deflexed head and broadly closed mid coxal cavities. Larvae differ from those of other scarabaeoids in having a darkly pigmented head with stemmata, 3 antennal segments and abdominal terga with transverse folds and stiff spines. Adults and larvae feed in dry animal remains, being one of the last in the succession of insects that invade carcasses. Larvae live in vertical burrows in the soil beneath the carcass. Adults stridulate by rubbing a plectrum on the penultimate abdominal segment against a file along the internal margins of the elytra. The group appears to flourish in the more arid parts of Australia; except for the introduced Holarctic *Trox scaber*, all Australian species belong to the genus *Omorgus*. [Scholtz 1986a, b]

**26. Geotrupidae** (Fig. 35.29A). ADULT: ANT 11(3), FCOX PROJ(CONC), FCAV CLOS(OPEN), MCOX CONT-NARR(OPEN), 5-5-5, ABD 6–7(0), 5–24 MM. LARVA: HEAD HYPO, STEM 0, ANT 3, FSUT 0, LABR FR, MOLA +, VMP PRO, GLAC, MP 4, LP 2, HSC +, HRD +, VER 0, LEGS 3, TS 0, UROG 0, SPIR CR.

Stout, very strongly convex beetles, yellowish to reddish brown, or rarely black, with prognathous head and usually with conspicuous cephalic and pronotal horns in male; antennal club relatively small and oval with closely appressed lamellae. Geotrupid larvae differ from those of other scarabaeoids in having a very lightly sclerotised head capsule and 3-segmented antennae. Except for the introduced *Geotrupes spiniger* (GEOTRUPINAE), all

Australian species belong to the BOLBOCERATINAE. Adults are often attracted to lights at night; they lay their eggs in deep burrows in the soil and provide the larvae with food which may include hypogean fungi, decaying organic matter or dung. Carne (1965) observed *Elephastomus meraldus* in the A.C.T. burying large quantities of cattle dung in its oviposition burrows, but dung feeding is not known in other bolboceratines. *G. spiniger*, on the other hand, uses dung for larval provisioning and was introduced into Australia for the control of cattle dung (p. 563). Bolboceratine larvae have all legs more or less reduced without a distinct claw and lack the stridulatory organs and complexly lobed anal region characteristic of *G. spiniger*. [H. F. Howden 1979, 1985; Howden and Cooper 1977; Howden and Peck 1987]

**27. Ceratocanthidae** (Acanthoceridae; Fig. 35.29C). ADULT: ANT 9–10(3), FCOX PROJ(CONC), FCAV CLOS(OPEN), MCOX CONT(OPEN), 5-5-5, ABD 5–6(0), 2.8–3.2 MM. LARVA: HEAD HYPO, STEM 0, ANT 4, FSUT 0, LABR FR, MOLA +, VMP PRO, GLAC, MP 4, LP 1, HSC +, HRD +, VER 0, LEGS 5, TS 0, UROG 0, SPIR CR.

Small and highly convex beetles with large head and pronotum, which can be strongly deflexed (as in Clambidae) so that mouth-parts, abdomen and parts of legs completely concealed, the body assuming a pill-like form. Scutellum very large and eye completely divided. Larvae distinguished from those of other scarabaeoids by 4-segmented antennae combined with multidentate labrum. The family is pantropical and the three Australian species, *Pterorthochaetes cribricollis*, *P. simplex*, and *Cyphopisthes descarpentriesi*, occur in northern Qld, where the last has been found in the nests of *Mastotermes darwiniensis* (ISOP). [Kistner 1982; Paulian 1977, 1978]

**28. Hybosoridae** (Fig. 35.29B). ADULT: ANT 10(3), FCOX PROJ(CONC), FCAV CLOS(OPEN), MCOX CONT(OPEN), 5-5-5, ABD 6–7(0), 4–15 MM. LARVA: HEAD HYPO, STEM 0, ANT 3, FSUT +, LABR FR, MOLA +, VMP PRO, GLAC, MP 4, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG 0, SPIR CR.

Shining, dark brown or black beetles, with sharply curved, acute mandibles, visible beyond strongly transverse labrum, and 10-segmented antennae with a club resembling that in Geotrupidae. Larvae similar to those of Ceratocanthidae, but with 3 lobes on labrum, 4th antennal segment highly reduced and fused to 3rd, and fore and mid legs forming stridulating organ. The Australian genera are *Liparochrus*, *Phaeochrous* and *Antiochrus*. Hybosorids are known to feed on carrion. [Allsopp 1984; Paulian 1980]

**29. Scarabaeidae** (Figs 35.30–33; Plates 4, D–F, L, M, O, P; 5, I). ADULT: ANT 7–10(3–7), FCOX PROJ(CONC), FCAV CLOS(OPEN), MCOX CONT-VWIDE(OPEN), 5-5-5, 6(0), 1.8–60 (3–50) MM. LARVA: HEAD HYPO, STEM 0/1, ANT 4/5, FSUT +, LABR FR, MOLA +, VMP PRO, GLAC/MALA, MP 4, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2/M, UROG 0, SPIR CR.

Usually stout-bodied beetles of moderate to large size; occasionally brightly coloured (few Melolonthinae, some Rutelinae, many Cetoniinae) or rarely small and clothed

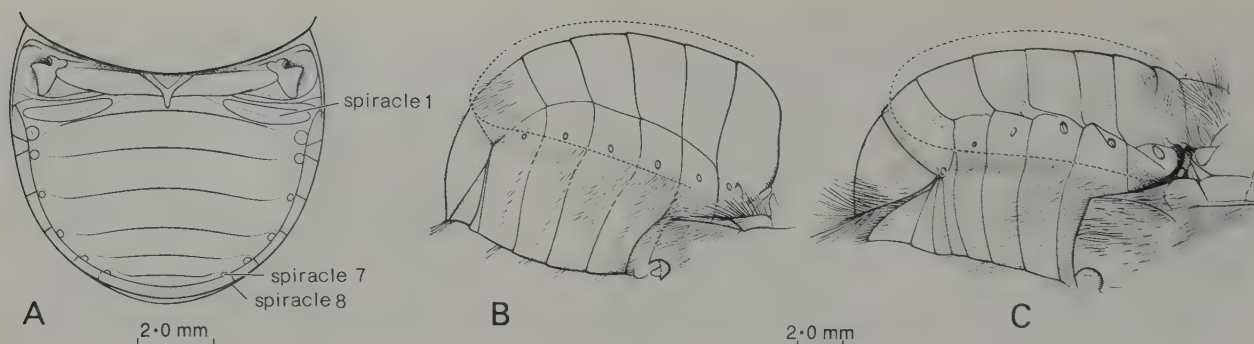


Fig. 35.30 Scarabaeoid abdomens (with elytra removed): A, liparostict type (*Onthophagus declivis*), dorsal; B, C, pleurostict types, lateral: B, Melolonthinae (*Colpochila* sp.); C, Rutelinae (*Anoplognathus* sp.). [F. Nanninga]

with scales (*Microvalgus*). With the exception of *Phaenognatha*, *Saprus* and certain Rutelinae, either the labrum or the mandibles are concealed from above by the clypeus, and in most cases both are concealed. Except in *Saprus*, exposed mandibles have non-opposable apices. The antennal club is variable but not cupuliform. Scarab larvae (Fig. 35.13B) always have 4 or apparently 5 antennal segments, and the legs are never modified as stridulatory organs; they always live in concealed habitats, feeding on roots, dung or decaying vegetable matter. [McQuillan 1985a]

*Keys to the Subfamilies of Scarabaeidae Known in Australia*

ADULTS

1. Tarsal claws unequal (at least on hind leg and usually on all legs, with one claw being more slender than the other or with one claw toothed and the other simple), often large, and movable (often held at different angles in dead specimens); elytra often with narrow membranous margin beneath posterolateral edge; pronotum always unarmed; cuticle often brightly coloured and metallic ..... RUTELINAE
- Tarsal claws equal, more or less fixed, and held at the same angle in dead specimens; elytra without narrow, membranous margin (sometimes with setal fringe) ..... 2
- 2(1). Abdominal spiracles located in pleural membrane, covered by elytra and not visible in intact insect (Fig. 35.30A); mid coxae strongly oblique or longitudinal; abdomen often shorter than metasternum; antennae with 8 or 9 segments ..... 3
- Spiracles diverging, so that several lie on abdominal sternites and at least one pair are exposed in intact insect (Figs 35.30B, C); mid coxae transverse or only slightly oblique; abdomen not shorter than metasternum; antennae often with 10 segments .... 5
- 3(2). Labrum exposed and about as long as wide; mandibles exposed with rounded, non-opposable apices; tarsi slender and very long, the hind tarsus in the male 3 to 4 times as long as the tibia (Fig. 35.31A); abdomen very hairy ..... ACLOPINAE
- Labrum concealed or slightly exposed and strongly transverse; mandibles concealed or slightly exposed with opposable apices; hind tarsi shorter and

- abdomen never hairy ..... 4
- 4(3). Hind tibiae with 2 apical spurs; mid coxae oblique and separated by less than their width; elytra usually completely concealing abdomen; scutellum present; more or less elongate beetles, very rarely with cephalic or pronotal armature ..... APHODIINAE
- Hind tibiae with 1 apical spur; mid coxae longitudinal and separated by more than their width; elytra always leaving pygidium exposed; scutellum almost always absent (present in *Thyregis*); more or less rounded beetles, usually with cephalic and/or pronotal armature in the male ..... SCARABAEINAE
- 5(2). Fore coxae conical, produced ventrally; mesothoracic epimera usually visible from above; antennal insertions exposed; mandibles concealed; dorsum somewhat flattened; usually brightly coloured ..... CETONIINAE
- Fore coxae transverse, not produced ventrally; mesothoracic epimera not visible from above; if antennal insertions slightly exposed, mandibles also exposed; dorsum more convex ..... 6
- 6(5). Mandibles at least partly visible from above (except in *Cryptodus* species, which are somewhat flattened and have the mouth-parts concealed from below by an enlarged mentum); usually at least 2 pairs of abdominal spiracles visible beneath edges of elytra; tarsal claws simple; head and/or pronotum in males often with tubercles, horns or complex elevations ..... DYNASTINAE
- Mandibles completely concealed from above; only 1 pair of abdominal spiracles visible beneath edges of elytra; tarsal claws often toothed; head and pronotum in males simple ..... MELOLONTHINAE

LARVAE

1. Apical antennal segment reduced, at most half as wide as penultimate segment, which bears a sensorium (pale oval spot) on inner side at apex; galea and lacinia distinctly separated for their entire lengths ..... 2
- Apical antennal segment about as wide as penultimate segment, which lacks a sensorium; galea and lacinia entirely fused, fused at base, or fitting very tightly together ..... 3
- 2(1). Legs 5-segmented, including a well-developed claw (tarsungulus); head capsule dark brown; body of



- normal grub shape, not humped ..... APHODIINAE
- Legs 2-segmented, without or with very small claws; head capsule usually yellow; body strongly humped (Fig. 35.31D) ..... SCARABAEINAE
- 3(1). Anal cleft Y-shaped or if transverse, then abdominal S9 with raster composed of bilaterally symmetrical, longitudinal or curved rows of setae separated by a bare area; mandible with ventral stridulatory area absent, indistinct or consisting of minute granules; galea and lacinia fused proximally or tightly fitting together ..... MELOLONTHINAE
- Anal cleft transverse; S9 without raster composed of bilaterally symmetrical rows of setae; mandible with ventral, oval stridulatory area consisting of a few to many transverse granular ridges; galea and lacinia entirely fused to form mala ..... 4
- 4(3). Labrum symmetrical, with deeply pigmented notch on each side of midline; head partly covered by prothorax; legs short, hind coxa shorter than width of clypeus; segments 9 and 10 partly fused, the suture between them incomplete dorsally ..... CETONIINAE
- Labrum asymmetrical with deeply pigmented notch on right side of midline; head more exerted; legs long, hind coxa longer than width of clypeus; segments 9 and 10 separated by complete suture ..... 5
- 5(4). Stridulatory teeth on dorsal edge of maxilla always with anteriorly directed points; apical antennal segment with 3 oval sensory areas; head never strongly punctured or dark brown ..... RUTELINAE

Stridulatory teeth on dorsal edge of maxilla bluntly rounded; apical antennal segment usually with more than 3 oval sensory areas; head usually strongly punctured, sometimes very dark brown ..... DYNASTINAE

ACLOPINAE are confined to Brazil, Argentina, Borneo and Australia. *Phaenognatha* (8 spp.) occurs in northern Qld and the N.T. Adults (Fig. 35.31A) are usually taken at light, and nothing is known of the biology (Allsopp 1981, 1983). APHODIINAE (Fig. 35.31B) tend to be smaller and more elongate than most scarabs, and with the exception of the Tasmanian *Saprus griffithi*, they have a membranous, concealed labrum. Of the 17 genera known from Australia, the largest are *Aphodius*, *Ataenius* and *Sapro-sites*. Most aphodiines are dung feeders, and some may be found in mammal nests and burrows. *Aphodius tasmaniae* is a phytophagous species, which is regarded as an important pasture pest; the larvae form vertical burrows from which they emerge at night to cut off leaves which they drag into their tunnels for consumption (Carne 1957a).

The SCARABAEINAE (dung beetles, Fig. 35.29A) is a large subfamily (more than 300 Australian species), the adults of which, like those of most aphodiines, have modified, liquid-feeding mouth-parts with a membranous, complexly setose labrum and lamellate, partly membranous mandibles; they differ from aphodiines, however, in being more robust and rounded in form, with widely

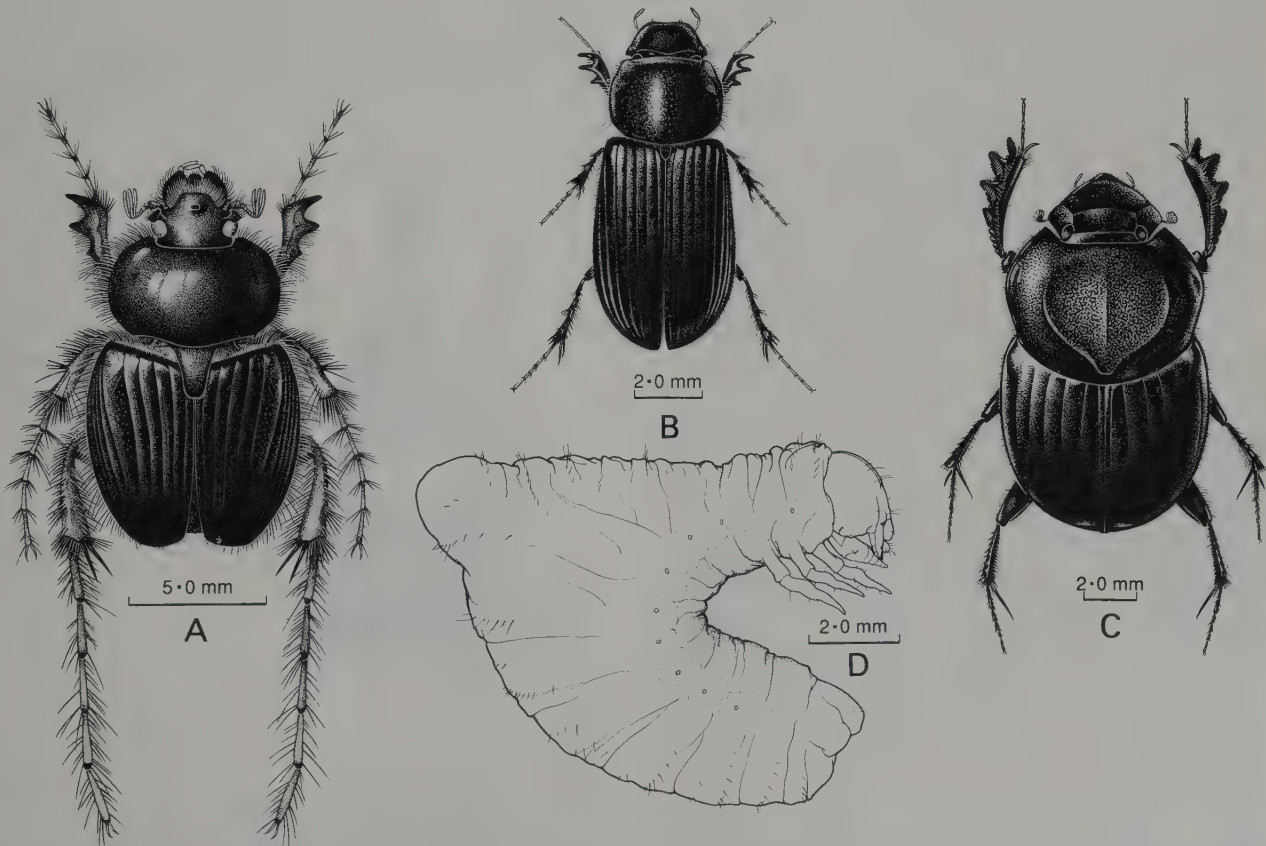


Fig. 35.31 Scarabaeidae: A, *Phaenognatha* sp., Aclopiniae; B, *Aphodius tasmaniae*, Aphodiinae; C, *Onthophagus declivis*, Scarabaeinae; D, *O. gazella*, larva. [A–C by F. Nanninga; D by A. Klinkenberg]



Fig. 35.32 *Sericesthis geminata*, Scarabaeidae-Melolonthinae.

[F. Nanninga]

separated mid coxae, an exposed pygidium, and usually conspicuous sexual dimorphism. Their larvae have a characteristic humped appearance and reduced legs. Scarabaeinae usually feed on the faeces of various animals and use this material as provisions for their larvae, which live in chambers or burrows in the ground, but details of feeding behaviour and nest construction are known for few Australian species (Bornemissza 1971a). Mycophagy is known in some *Onthophagus* (Bornemissza 1971b), and species of *Cephalodesmius* have been shown to form brood balls from dead leaves and other plant material, rather than dung (Monteith and Storey 1981). Although many scarabaeines build their brood chambers directly beneath the food source, some (ball-rollers) form a ball of dung, push this away from the dung mass, and form their brood chambers at some distance from the food source. The native Australian fauna comprises 20 genera placed in 3 of the 6 known tribes: Scarabaeini (e.g. *Amphistomus*, *Cephalodesmius*, *Lepanus*, *Temnoplectron*), Coprini (e.g. *Coptodactyla*, *Demarziella*), and Onthophagini (*Onthophagus*), but species of *Copris* (Coprini), *Sisyphus* (Scarabaeini), *Onitis* (Onitini) and *Euoniticellus* (Oniticellini), as well as additional species of *Onthophagus*, have been introduced from South Africa and the Mediterranean Region for the biological control of cattle dung (p. 563). *Onthophagus* is our largest genus, with almost 200 species, and a few are remarkable in that the adults have prehensile claws and cling to the hair around the anus of wallabies. [Halfpter and Edmonds 1982; Matthews 1972–76; Matthews and Stebnicka 1986]

Adult MELOLONTHINAE (Fig. 35.32; Plate 5, I) are usually called chafers and are often reddish brown in colour, but may be black, or sometimes metallic or bicoloured. The C-shaped, soil-dwelling larvae, commonly known as

white grubs, feed on roots and other organic matter and may cause serious damage to vegetables, wheat, sugar cane and pastures. Pupation occurs in a cell at some depth in the soil, and the adult, after eclosion, remains in the cell until rain softens the soil. This synchronises adult emergence and flight. Most adults are crepuscular or nocturnal and many, including *Sericesthis geminata*, *Heteronyx*, *Automolus* and *Liparetrus*, feed on leaves and may be serious tree defoliators. Common diurnal forms include the metallic species of *Diphucephala* and bicoloured species of *Phyllotocus*, which may swarm around flowering trees and shrubs. Some *Maechidius* occur in termite nests. The profusion of species of Melolonthinae may be explained by temporal isolation resulting from local rainfall in semidesert areas. Special features which might lead to the isolation of limited populations in time are: a) the short adult life, b) the fact that adults remain in pupal cells until released by rain, c) the duration of the life cycle, which is often more than one year, d) the fact that adults, though winged, fly only short distances, and e) the fact that some species do not feed as adults. [Britton 1957, 1978, 1980, 1986, 1987]

RUTELINAE (Plate 4, D–F, L, M) are of stout build and are usually brightly coloured and metallic. Larvae are similar to those of melolonthines and also occur in soil; those of some species of *Anoplognathus* cause damage to lawns and pastures, and adults of the same genus, commonly called Christmas beetles, often defoliate eucalypts. [Carne 1957b, 1958]

DYNASTINAE (Figs 35.33A–C) are stout bodied, mainly black or brown and often exhibit obvious sexual dimorphism, the males bearing horns or tubercles which are disproportionately large in larger specimens (allometry)

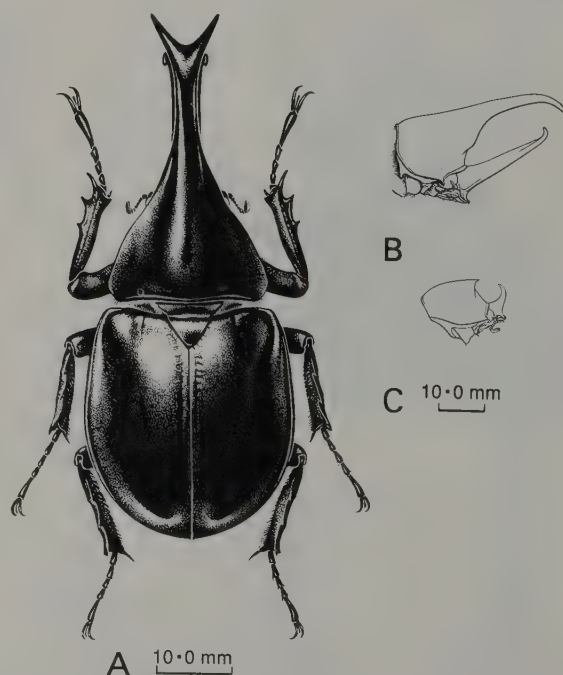


Fig. 35.33 *Xylotrupes gideon*, Scarabaeidae-Dynastinae, ♂; B, C, same, profile of head and prothorax showing variation of form with size in males. [F. Nanninga]



(Figs 35.33B, C). Larvae feed on roots or decaying vegetable matter in soil or rotten logs, and the nocturnal adults do not feed on leaves. The subfamily includes several well-known soil pests, including *Heteronychus arator*, introduced from South Africa. Species of the largest genus, *Cryptodus*, live in association with ants and termites. The subfamily is most abundant and diverse in the north and west of the continent, and includes some of our largest beetles, such as *Haploscapanes barbarossa*. [Carne 1957c; Endrödi 1985]

CETONIINAE (Plate 4, O, P) include a number of somewhat flattened beetles, which have exposed mesepimera and pygidium and usually a strikingly patterned, metallic or 'enamelled' colouring. Adults are diurnal nectar feeders, and can fly rapidly by spreading their wings without the necessity of raising the elytra. Larvae occur in rotten wood or decaying vegetation, and normally are able to move on their backs, even on the surface of the soil, by using the tergal folds, which are densely clothed with strong bristles. *Microvalgus* differs from most members of the subfamily in being less than 5 mm in length and clothed with scale-like setae; little is known of its habits but larvae may be associated with termites. Some of the common or well-known Cetoniinae include *Eupoecila australasiae*, *Diaphonia*, *Chlorobapta* and *Lomaptera*. [Krikken 1984]

### Series ELATERIFORMIA

This series is used in the sense of Lawrence (1988b) and differs from Crowson's Elateriformia in the inclusion of Dascilloidea. Larval similarities between scarabaeoids and Dascillidae are either plesiomorphic or associated with soil-dwelling habits, and adult dascilloids share many more features with elateriform taxa such as Buprestidae, Callirhipidae and Ptilodactylidae (Lawrence and Newton 1982). A general feature shared by many members of the series is the heterogeneous life cycle, with long-lived larvae and short-lived adults usually occupying different habitats. Surface-active adults often have a streamlined body and complex pro-mesothoracic interlocking device, or in its absence, a chemical defence system and aposematic coloration. The antennae are rarely clubbed and often serrate, and with the exception of derived, soft-bodied forms, the hind coxae are more or less excavate to receive the femora.

### Superfamily DASCILLOIDEA

Although Dascillidae and Rhipiceridae share several adult features, such as the type of prothoracic interlocking device, metendosternite, wing venation, wing folding, and aedeagus, rhipicerid larvae differ from those of dascillids and resemble more derived elateriform larvae in having consolidated ventral mouth-parts, biforous spiracles and no mola. [Crowson 1971a]

**30. Dascillidae** (Fig. 35.34). ADULT: ANT 11(SER), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-5, ABD 5(0-2), 7.5-12 mm. LARVA: HEAD HYPO, STEM 0, ANT 2A/3, FSUT 0, LABR PF, MOLA +, VMP RET, GLAC, MP 3, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS M, UROG +, SPIR CR.

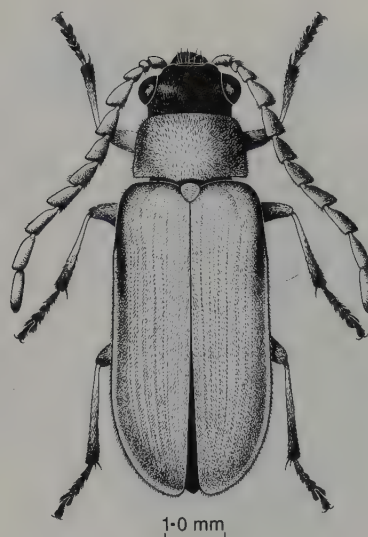


Fig. 35.34 *Notodascillus sublineatus*, Dascillidae.

[F. Nanninga]

Elongate, more or less parallel-sided beetles, brown and clothed with decumbent grey or yellow pubescence which usually forms narrow stripes on the elytra. They differ from the closely related Rhipiceridae in having serrate antennae, which are not borne on tubercles, and a strongly transverse pronotum with complete lateral carinae visible from above, and in lacking an empodium between the tarsal claws. Larvae are similar to those of Scarabaeoidea in being more or less C-shaped, with a large head, well-developed legs, and complex epipharyngeal and hypopharyngeal armature, but they differ from them in having the labrum partly fused to the clypeus, the antennae appearing to be 2-segmented with the sensorium at the apex, and T9 with a pair of minute urogomphi. Dascillid larvae live on organic matter in the soil, and some Holarctic species are known to damage roots. *Notodascillus* (2 spp.) occurs in northern N.S.W. and southern Qld.

**31. Rhipiceridae** (Fig. 35.35). ADULT: ANT 11/20 + ♂ (PECT-FLAB ♂), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-5, ABD 5(2), 10-25 mm. LARVA: HEAD PRO(PRO), STEM 0, ANT 1/3, FSUT 0, LABR FU, MOLA 0, VMP RET, GLAC, MP 1/2, LP 1, HSC 0, HRD 0, VER 0, LEGS 3-5, TS 0/1, UROG 0/+, SPIR AN/AB.

Adults are easily recognised by the multisegmented, flabellate antennae in the male (pectinate in female) and membranous lobes on tarsal segments 1-4. Unlike the closely related Dascillidae, they have weak lateral pronotal carinae, which are incomplete anteriorly and barely visible from above, antennae borne on raised tubercles, and a large, setose empodium. The male antennae are unique in having more than 20 segments. Larvae are unknown for Australian species, but those of the North American *Sandalus niger* are lightly sclerotised ectoparasitoids of immature cicadas (HEMI) and have a minute triungulin-like 1st instar (Elzinga 1977). Australian species all belong to *Rhipicera*.

Fig. 35.35 *Rhipicera femorata*, Rhipiceridae.

[F. Nanninga]

### Superfamily BUPRESTOIDEA

The phylogenetic relationships of the family Buprestidae have been the subject of some controversy, and the group is usually placed in a monotypic superfamily. Forbes (1926, 1942) noted similarities in the wing folding of schizopodine buprestids and members of the Dascilloidea; while Crowson (1982) pointed out a number of features shared by Buprestidae and members of the dryopid complex (Dryopidae, Elmidae, Lutrochidae, Limnichidae, Heteroceridae). Lawrence (1988b) suggested that the family could be the sister group of the Byrrhoidea (see below), but an equally convincing case might be made for the derivation of buprestids directly from a dascilloid ancestor.

**32. Buprestidae** (jewel beetles; Plates 4, T, V–ZA; 6, E). ADULT: ANT 11(SERR–PECTR), FCOX GLOB (EXP), FCAV OPEN(OPEN), MCOX VWIDE(OPEN), 5-5-5, ABD 5(2), 1.5–65 (5–40) MM. LARVA: HEAD PRO(RET), STEM 0/2, ANT 2, FSUT +, LABR FR, MOLA 0, VMP PRO, MALA, MP 2, LP 0/1, HSC 0, HRD 0, VER 0, LEGS 0/+R, TS 0, UROG 0, SPIR CR.

Heavily sclerotised, rigid beetles, usually elongate and brilliantly coloured with metallic sheen. Head more or less globular, deflexed, and deeply sunk into prothorax, which is closely applied to elytra; antennae short and usually serrate, eyes large, reniform and not very protuberant; mesosternum with large cavity for reception of prosternal process; metasternum with well-marked transverse suture; tarsi with membranous lobes beneath segments 1–4 and no empodium; abdominal tergites heavily sclerotised; first 2 ventrites solidly fused, suture between them indistinct or incomplete; aedeagus distinctive in having the phallobase fused to parameres and latter partly or completely fused together; Malpighian tubules cryptonephridial (unique in Elateriformia). Larvae (Fig.

35.39A) soft bodied, with prothorax markedly expanded and flattened (except in minute leaf-miners); antennae very short; abdominal apex simple or bearing paired appendages on segment 10 (Agrilinae). Adults are active in hot weather and will readily fly in sunlight; they often occur in nectar-bearing flowers. Larvae usually feed in the wood (often in the phloem just beneath the bark) or root systems of trees or shrubs, but some feed in herbaceous stems or galls or mine leaves.

The Australian fauna includes members of about half of the subfamilies and tribes known for the world; these are keyed out by Bellamy (1986). The POLYCESTINAE include, among others, *Astraeus* and *Prospheres*, while MASTOGENIINAE are represented by *Helferella*. Among the CHALCOPHORINAE are the primitive, conifer-feeding *Diadoxus* and *Araucariana*, the large tropical *Cyphogastra* (Plate 4, V) and *Pseudotaenia* (Plate 4, Y), and the largest of Australian buprestids, *Julodimorpha bakewelli*, a mallee species most common in W.A. and known for its habit of congregating around 'stubby' beer bottles (Gwynne and Rentz 1983). The BUPRESTINAE include *Bubastes*, *Nascio*, *Melobasis* and *Curis* plus the Stigmoderini (*Stigmodera*, *Themognatha*, *Castiarina* and their relatives), containing almost half of the described species. *Stigmodera* are often aposematically coloured, and these and other members of the family often contain bitter chemicals called buprestins (Brown *et al.* 1985; B. P. Moore and Brown 1989). Among the CHRYSOBOTHRINAE are *Chrysobothris* and *Merimna atrata*, which is known as the fire beetle, because of its habit of flying to burnt trees. The AGRILINAE is a large group of smaller species, some of which are gall-makers; the largest included genus is *Cisseis*. The TRACHYINAE include small leaf-miners in *Habroloma* and *Trachys*. [S. Barker 1986; Carnaby 1987; Carter 1929; J. A. Gardner 1990; Hawkeswood 1985; Hawkeswood and Peterson 1982]

### Superfamily BYRRHOIDEA

Byrrhoidea, as used here, includes Byrrhoidea plus Dryopoidea, in the sense of Crowson (1960, 1973b, 1978, 1982), Callirhipidae from the Artematopoidea (Crowson 1973b), Cneoglossidae from the Cantharoidea (Crowson 1972b), and Byrrhoidea plus Psephenioidea of Lawrence (1988b). The group is variable and not easily characterised using either adult or larval features. Adults have a specialised, high-grade type of wing folding (dryopoid type of Forbes 1926), which has been modified subsequently in large, elongate forms (Callirhipidae, Eulichadidae) to resemble that found in most elateroids (Kukalová-Peck and Lawrence, unpubl.). Byrrhoid larvae usually have a single tarsungular seta; but those of Byrrhidae have 2, Eulichadidae have several and Callirhipidae have none. Aquatic and riparian habits are common in several families, and many special respiratory features (anal gills, abdominal gills, dorsally or posteriorly projecting 8th spiracles, plastron plates) have evolved in larvae of Dryopidae, Lutrochidae, Elmidae, Limnichidae, Psephenidae, Eulichadidae and Ptilodactylidae. Other attributes which have evolved in two or more byrrhoid lineages are loss of the 8th abdominal



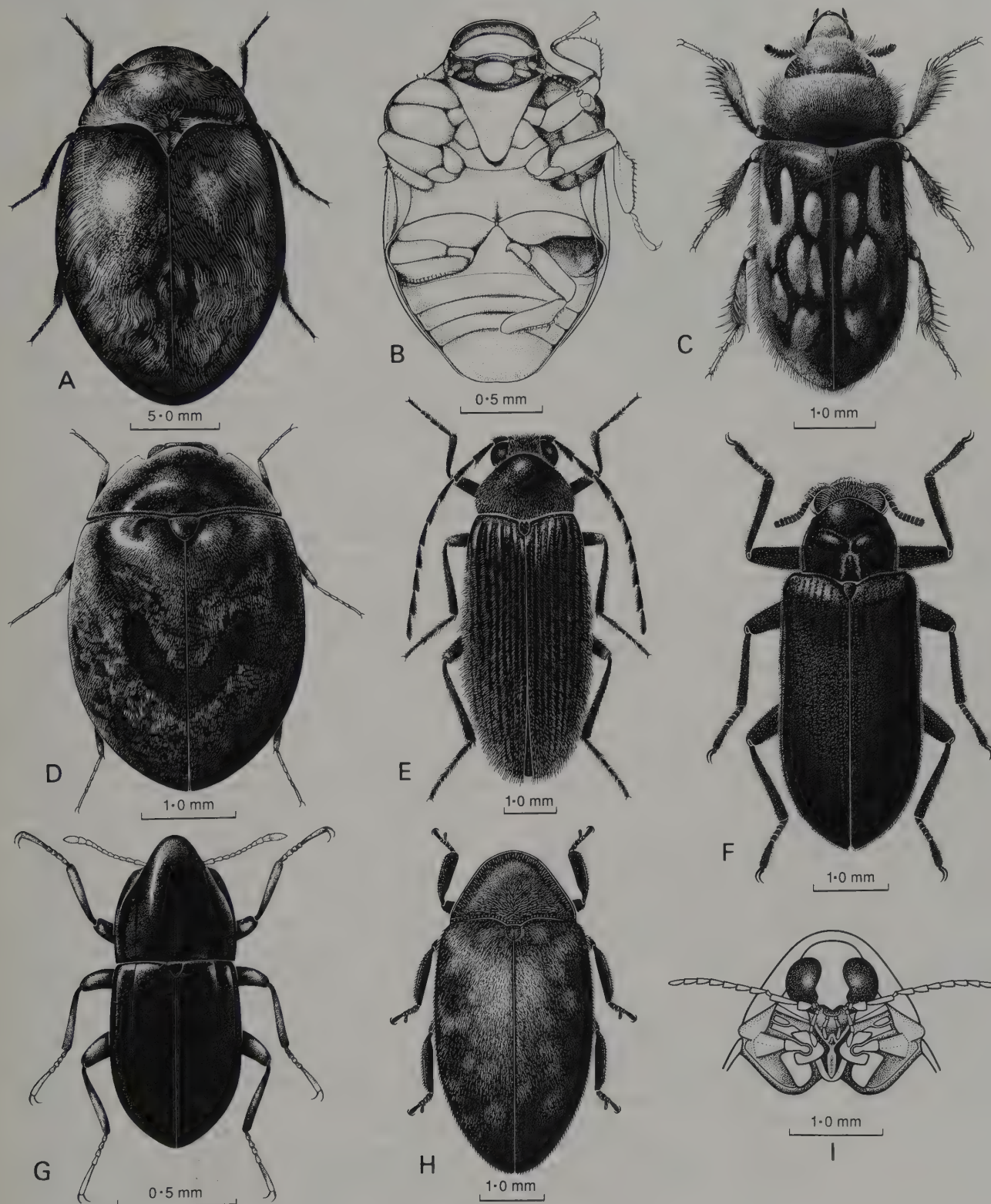


Fig. 35.36 Elateriformia: A, *Limnichus australis*, Limnichidae; B, *Microchaetes* sp., Byrrhidae, ventral showing cavities for reception of legs; C, *Heterocerus flindersi*, Heteroceridae; D, *Sclerocyphon* sp., Psephenidae; E, *Byrrhocryptus oblongus*, Ptilodactylidae; F, *Stetholus elongatus*, Elmidae-Larainae; G, *Austrolimnius waterhousei*, Elmidae-Elminae; H, *Chelonarium australicum*, Chelonariidae; I, same, head, prothorax and mesothorax, ventral.

[A, C–E, G by F. Nanninga; B by S. Smith; F, H, I by S. P. Kim]



spiracles and development of a heavily sclerotised ovipositor in the adult and coaptation of the maxillolabial complex and development of an operculum in the larva. The family Dryopidae is not known to occur in Australia, but it has been included in the key because of the presence of the dryopid genus *Elmomorphus* in Papua New Guinea (Satô 1973).

**33. Byrrhidae** (Figs 35.36B, 39B, Plate 5, H). ADULT: ANT 11(INCR/1-5), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX MWIDE-VWIDE(OPEN), 5-5-5/4-4-4, ABD 5(2-3), 1.5-5.5 mm. LARVA: HEAD HYPO, STEM 6, ANT 3, FSUT +, LABR FR, MOLA 0, VMP RET, GLAC, MP 4, LP 2, HSC 0, HRD 0/+, VER +, LEGS 5, TS 2, UROG 0, SPIR BI.

Short, stout, strongly convex beetles, lacking transverse metasternal suture and with deflexed head, broad prosternal process which fits into a cavity on mesosternum, legs which may be capable of retraction into ventral cavities (Fig. 35.36B), and tarsi which usually bear a membranous appendage on segment 3 and which may fit into grooves on tibiae. Most Australian species are placed in *Microchaetes* and *Pedilophorus*, but the latter is a composite of several taxa for which names are not yet available. *Microchaetes* is dull black, tuberculate and clothed with stiff bristles or scales; larvae (Fig. 35.39B) are cylindrical and lightly sclerotised, with a concave plate at the abdominal apex. '*Pedilophorus*' are either glabrous or clothed with mixed setae and are usually metallic green; their larvae are onisciform with a heavily sclerotised dorsal surface. The most striking species is the Tasmanian *P. gemmatus* (Plate 5, H), which is metallic green with red bosses on the elytra. Adult and larval byrrhids are usually found feeding on mosses or liverworts, but some may also occur among the roots of higher plants. An undescribed '*Pedilophorus*' from Mt Kosciuszko feeds on the rosettes of *Cardamine* (Brassicaceae) and transmits the turnip yellow mosaic virus (TYMV-Cd) (Guy and Gibbs 1985). [Lea 1920]

**34. Elmidae** (Helminthidae, Elminthidae: Figs 35.36F, G, 39C, D). ADULT: ANT 11(FIL-INCR), FCOX TRANS-GLOB(EXP-CONC), FCAV OPEN(OPEN), MCOX MWIDE-VWIDE(OPEN), 5-5-5, ABD 5(3), 0.9-6 mm. LARVA: HEAD PRO(PRO), STEM 1/5, ANT 3, FSUT +, LABR FR, MOLA 0, VMP RET, GLAC, MP 4, LP 2, HSC 0, HRD 0, VER +, LEGS 5, TS 1, UROG 0, SPIR BI/RED.

Small to minute, darkly pigmented beetles, with moderately short, slender or slightly incrassate antennae, moderately to widely separated coxae, and long legs with simple tarsi and long claws. Larvae (Figs 35.39C, D) onisciform to cylindrical, with movable operculum and paired hooks on S9 and 3 pairs of retractile anal gills. Adult ELMINAE (Fig. 35.36G) are glabrous or sparsely pubescent above but have ventral tomentose tracts which serve as a plastron (Fig. 2.14); adult LARAINAE (Fig. 35.36F) are densely pubescent but lack a ventral plastron. Most adult elmids and all larvae live under water, usually in lotic habitats with rocky bottoms, clear water and higher oxygen content, and feed on decaying vegetation or algae. Larvae breathe through the anal gills, but they possess

functional spiracles in the last instar, when they leave the water to pupate. Most adults are capable of remaining under water for long periods by maintaining an air bubble. Australian Larainae include *Hydora*, *Ovolara*, *Stetholus* and *Potamophilinus*, while the Elminae are placed in several genera, the largest of which are the endemic *Simsonia*, *Notriolus* and *Kingolus*, and *Austrolimnius*, which also occurs in South America. Larvae of several Australian elmids have been reared but not yet described (Glaister 1985). [H. P. Brown 1981, 1987; Hinton 1965, 1968; Stride 1955]

**35. Limnichidae** (Fig. 35.36A). ADULT: ANT 11(FIL/INC/3/4), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX VWIDE(OPEN), 5-5-5 4-4-4, ABD 5(3/5), 0.9-4.5 mm. LARVA: HEAD PRO(PRO), STEM 5/6, ANT 3, FSUT +, LABR FR, MOLA 0, VMP RET, GLAC, MP 4, LP 2, HSC 0, HRD 0, VER +, LEGS 5, TS 1, UROG 0, SPIR BI.

Very small, oval and moderately convex beetles, clothed with decumbent, erect or occasionally minute and pruinose vestiture. They resemble some Byrrhidae in having ventral cavities into which legs can be folded, but they differ from byrrhids in being much less convex and usually by having slender antennae, a longer prosternum which extends well in front of the coxae, a distinct transverse metasternal suture, and a frontoclypeal suture. *Paralimnichus* lacks the transverse metasternal suture and has lobed tarsi similar to those in byrrhids, but differs from them in having all 5 ventrites connate and the eyes deeply emarginate. *Pseudeucinetus* has a short prosternum, but it is distinguished by the large, oblique hind coxae and dorsally placed eyes. This genus and *Hyphalus* also differ from other limnichids in having 4-segmented tarsi. Limnichid larvae are cylindrical and resemble some kinds of byrrhid larvae, but they are easily distinguished from them by having the maxillolabial complex consolidated, so that the cardines are contiguous, the maxillary articulating areas are absent and the postmentum is joined to the stipites for most of its length.

The Australian fauna is relatively rich, but few species have been described. Many northern species belong to the tropical genus *Byrrhinus*, but several other genera are represented. *Hyphalus* occurs in interstices of intertidal coral slabs on the Great Barrier Reef, and is also known from Lord Howe I., Norfolk I., New Zealand and the Cocos-Keeling Islands. Limnichids often occur in riparian situations and large numbers may be attracted to lights at night. Larvae usually live in sand, mud and leaf litter, and apparently feed on decaying organic matter. *Hyphalus* larvae have anal gills for living submerged during high tides. [Britton 1971, 1977; Lawrence 1987a; Paulus 1970; Spilman 1959]

**36. Heteroceridae** (Fig. 35.36C). ADULT: ANT 11(SERR/PECT/INCR), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX CONT-MWIDE(OPEN), 4-4-4, ABD 5(3), 2.2-5.3 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT +, LABR FR, MOLA PS, VMP RET, GLAC, MP 3, LP 2, HSC 0, HRD 0, VER +, LEGS 5, TS 1, UROG 0, SPIR CR(SP).

Elongate, densely pubescent beetles, with maculate



elytra, prognathous head, large labrum, thick antennae, flattened, spinose tibiae and simple tarsi. Larvae elongate, tapered posteriorly, and clothed with scattered, dark, erect setae; mandibles flattened with a sub-basal, concave mola; ventral mouth-parts consolidated; S10 forming conical pygopod. Heterocerids tunnel in mud at the edges of ponds and streams and apparently subsist on algae, diatoms and organic debris. The Australian fauna consists of the rare and unusual *Elythomerus elongatulus* from Qld and several species currently placed in *Heterocerus*. [Charpentier 1968]

**37. Psephenidae** (Figs 35.36D, 39G). ADULT: ANT 11 (FIL/SER), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-5, ABD 5(3), 2.8-8 MM. LARVA: HEAD PRO(PRO), STEM 6, ANT 3, FSUT +, LABR FR, MOLA 0, VMP RET, GLAC, MP 3/4, LP 2, HSC 0, HRD 0, VER 0, LEGS 5, TS 1, UROG 0, SPIR RED/SP.

Broadly oval, flattened beetles clothed with short, dense pubescence forming pattern which is superimposed on maculate dorsal surface. Head deflexed and only partly visible from above within anterior pronotal emargination, and bases of pronotum, scutellum and elytra finely crenulate forming interlocking device. Head narrowed anteriorly forming a short rostrum; mouth-parts usually concealed by prosternal chin piece; prosternal process fits into mesosternal cavity; metasternal transverse suture distinct; tarsi long and simple. Larvae (Fig. 35.39G) broadly oval, strongly flattened and disc-like, with head and legs concealed from above, and disc clothed with pattern of granules and modified setae, lined with marginal fringe of hairs, and provided with 2-4 pairs of defensive gin traps (p. 559). Antennae long; labrum large; maxillae freely movable but partly concealed behind expanded postmentum. Functional spiracles on segment 8 in final instar only; spiracular brush on T9 opposite each spiracle prevents silt from clogging opening; S9 with movable operculum, concealing chamber which houses paired retractile anal gills.

The family is represented in Australia by *Sclerocyphon*, which is most closely related to the Chilean *Tyche-psephus*. These genera belong to the widespread subfamily EUBRIINAE. Larval psephenids are commonly found adhering to rocks in streams throughout the wetter parts of eastern Australia, but one species has also been recorded from the George Gill Ranges in the central part of the continent. Larvae feed on algae covering rocks, and because of their unique, streamlined form, they are able to move across surfaces within high energy water flows and thus exploit resources unavailable to their competitors. Pupation takes place within the larval skin in concealed areas along the stream bank. Adults are very cryptic, but they have been observed flying above streams on hot days. [J. A. Davis 1986; Hinton 1955a, 1966b]

**38. Callirhipidae** (Figs 35.37A, B). ADULT: ANT 11 (PECT/FLAB♂), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-5, ABD 5(3), 9-23 MM. LARVA: HEAD HYPO, STEM 0, ANT 1, FSUT +, LABR FR, MOLA 0, VMP RET, MALA, MP 4, LP 2, HSC 0, HRD 0, VER +, LEGS 5, TS 0, UROG 0, SPIR BI.

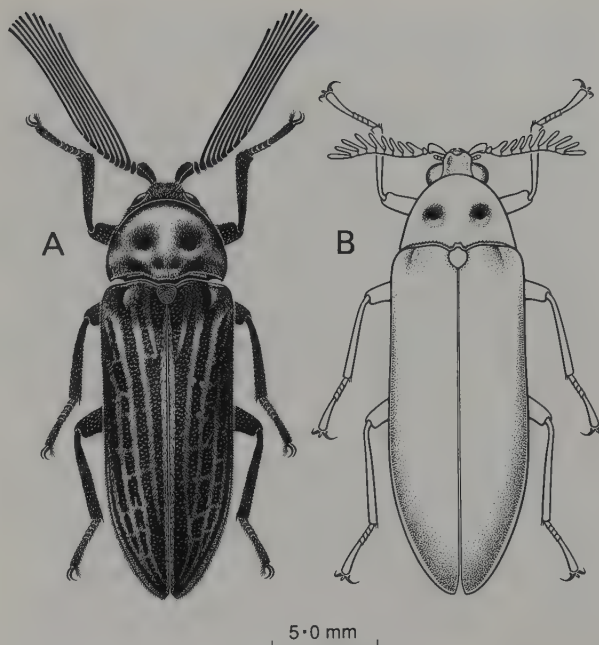


Fig. 35.37 *Callirhipis cardwellensis*, Callirhipidae: A, ♂; B, ♀. [S. P. Kim]

Large, elongate beetles with prominent antennae borne on frontal prominence and pectinate (female) or flabellate (male) beginning with the 3rd segment. Eyes large and projecting; prothorax without distinct lateral carinae and with well-developed basal interlocking mechanism, which may be crenulate; elytra ribbed or provided with window punctures; tarsi simple with large, multisetose empodium between claws. Larvae heavily sclerotised and cylindrical, with globular head, very short antennae, solidly fused maxillolabial complex, sclerotised ligular plate, short legs, and dorsally-hinged operculum at abdominal apex. Australian species belonging to *Callirhipis* and *Ennometes* occur in wet forests of northern N.S.W. and Qld. Larvae live in rotten logs, and adults have been collected at light.

**39. Ptilodactylidae** (Figs 35.36E, 39E, F, J). ADULT: ANT 11(FIL/SERR/PECT), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-5/P4-4-4, ABD 5(3), 2.5-8.5 MM. LARVA: HEAD PRO(PRO), STEM 1/5/6, ANT 3, FSUT 0/+, LABR FR, MOLA 0, VMP RET/PRO, GLAC, MP 4, LP 2, HSC 0, HRD 0, VER +, LEGS 5, TS 1, UROG 0/+, SPIR BI/RED.

Elongate, pubescent beetles with moderately long antennae, sometimes bearing narrow, articulated appendages attached to bases of segments 4-10. Head strongly deflexed; pronotum with sharp lateral carinae, which are almost always incomplete anteriorly, and strongly developed basal interlocking mechanism with crenulations; scutellum notched anteriorly; elytra often striate; tarsi simple, provided with ventral brushes, or sometimes with reduced 4th segment and membranous appendage on 3rd. The Australian fauna includes *Byrrhocryptus*, with several species distributed along the east coast and related species in New Zealand, *Ptilodactyla*, with a few species in North

Qld, and an undescribed genus related to the Holarctic *Paralichas*. Adults are not common but may be collected at light.

There are three larval types, all of which feed on decaying plant material. The aquatic larvae of *Byrrhocraptus* (Figs 35.39E, F, J) are elongate and subcylindrical, with long antennae, a mandible bearing 2 brushes of hairs at base, movable maxillae with the articulating area partly concealed behind the postmentum, which is expanded and longitudinally divided into 3 parts, paired gular sutures, laterally placed abdominal spiracles, T9 forming a sclerotised, concave plate, and segment 10 with a pair of lobes bearing several hooks and usually 2 osmoregulatory papillae. *Ptilodactyla* larvae, which occur in leaf litter and wet rotten wood, are more curved ventrally at apex, and have an articulated process at the mandibular base, an undivided postmentum, fused gular sutures, paired lateral defence glands on mesothorax and segment 8, no anal papillae and fewer anal hooks. The third larval type, which is also found in leaf litter, has simple mandibles, an undivided postmentum, very short antennae, the 8th spiracles placed at the end of a posteriorly projecting process, and S9 with a ventral operculum. [Lawrence 1987a, 1988b; Stribling in press]

**40. Chelonariidae** (Figs 35.36H, I). ADULT: ANT 11(FIL/SERR), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX MWIDE(OPEN), 5-5-5, ABD 5(3), 5.5-5.8 MM. LARVA: HEAD PRO(PRO), STEM 1, ANT 3, FSUT +, LABR FR, MOLA 0, VMP RET, MALA, MP 4, LP 2, HSC 0, HRD 0, VER +, LEGS 5, TS 1, UROG 0, SPIR SP.

Oval, lenticular, highly compact beetles with a strongly deflexed head not visible from above and legs capable of being retracted into cavities on ventral surface. Labrum and mandibles highly reduced and concealed; antennae with 2nd and 3rd segments enlarged, 4th minute and last 7 slender and weakly serrate; pronotum with continuous carina formed from lateral carinae, and anterior edge and basal interlocking device with crenulations; prosternum highly reduced; mesosternum with large cavity for receiving prosternal process; metasternal transverse suture absent; elytra with narrow epipleural grooves which interlock with pterothorax and abdomen; tibiae flattened and provided with external spines; tarsi with segment 4 reduced, 3 with membranous appendage beneath it; tarsal claws toothed. Larvae elongate, posteriorly narrowed and clothed with tubercles and long, pubescent hairs. Head globular with long epicranial stem; mandibles simple at base; sutures absent between the maxillae and labium; S9 with ventrally-hinged operculum; spiracles are of unique, undulating type borne on lateral tubercles. The only Australian species is *Chelonarium australicum* from North Qld.

### Superfamily ELATEROIDEA

This superfamily includes most of the Cantharoidea and Elateroidea in the traditional sense, plus Rhinorhipidae, Brachypsectridae and Artematopidae. All elateroid adults lack a mandibular mola and transverse metasternal suture and have a low grade type of wing folding (Hammond

1979), and all but Rhinorhipidae have only 4 Malpighian tubules. Known larvae have a single large stemma on each side of the head (sometimes absent) and a feeding mechanism adapted for liquid feeding (mola absent, ventral mouth-parts connate, buccal cavity blocked by hairs). The exotic family Artematopidae has a very primitive type of wing folding (Forbes 1926), which suggests a more basal position within the Elateriformia.

**41. Rhinorhipidae** (Fig. 35.38H). ADULT: ANT 11(FIL), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-5, ABD 5(3), 5-8.5 MM. LARVA: UNKNOWN.

Elongate, dull-coloured, pubescent beetles with moderately long antennae, strongly deflexed head, an elongate and narrow clypeus and concealed, membranous labrum, a relatively narrow prothorax without lateral carinae, broad metepisterna and no transverse metasternal suture, large hind coxae with well developed vertical faces, moderately stout and tuberculate tibiae, the hind pair of which are expanded apically, and simple tarsi with pectinate claws. Females differ from males in being somewhat stouter with shorter antennae. The single species *Rhinorhipus tamborinensis* has been collected only in early spring (late October) at higher elevations in southern Qld. Males are relatively common during the day on low foliage bordering rainforest, and when disturbed feign death and drop to the ground; females are rare in the same situations. [Lawrence 1988b]

**42. Brachypsectridae** (Fig. 35.39H). ADULT: ANT 11(INCR/PECT♂), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-5, ABD 5(0), 5-7 MM. LARVA: HEAD PRO(PRO), STEM 1, ANT 2A/3, FSUT 0, LABR FU, MOLA 0, VMP RET, GLAC, MP 4, LP 2, HSC 0, HRD 0, VER 0, LEGS 5, TS 2, UROG 0, SPIR AN.

Oblong, somewhat flattened, yellowish brown beetles with hind angles of pronotum acute and carinate and prosternum long, forming a chin piece beneath head. Antennae relatively short with apical segments slightly enlarged in female but with last 6 or 7 segments forming weakly pectinate club in male. Mandibles reduced; elytra weakly striate; tarsi simple; ventrites free. Larvae strongly flattened and ovate, with complex lateral processes on all thoracic segments and abdominal segments 1-8 and with segment 9 produced posteriorly to form flexible, tapered spine. Head prognathous, with one pair of large stemmata, club-like antennae that appear 2-segmented, free but reduced labrum, perforated, falcate mandibles, and strongly consolidated ventral mouth-parts, with fused cardines and only partial sutures between postmentum and stipites. Thoracic spiracles are biforous, but those on the abdomen are reduced and annular. The only included genus *Brachypsectra* occurs in North America, India, Malaysia and northern Australia, where larvae of an undescribed species were taken in Winjana Gorge, W.A. In south-western North America, larvae of *B. fulva* tend to remain motionless under loose bark or in rock crevices; when spiders or other small arthropods walk over the flattened body, perhaps attracted by an allomone, the larva pins the prey between the flexible head and tail



spine and proceeds to pierce the cuticle and feed by extraoral digestion. Adults are rare and those of the Australian species have never been collected. [Blair 1930; Crowson 1973b; Lawrence 1991]

**43. Eucnemidae** (Fig. 35.38F). ADULT: ANT 11(FIL/SERR/PECT/FLAB), FCOX GLOB (CONC), FCAV OPEN(OPEN), MCOX MWIDE(OPEN), 5-5-5, ABD 5(5), 2.3–18 MM. LARVA: HEAD PRO(PRO), STEM 0, ANT 2, FSUT 0, LABR FU, MOLA 0, VMP RET/PRO, MALA 0, MP 0/2/3, LP 0/1/2, HSC 0, HRD 0/+, VER 0, LEGS 0, TS 0, UROG 0/+R, SPIR BI.

Elongate, cylindrical to slightly flattened, compact beetles, usually finely pubescent and with acute posterior angles on pronotum. They closely resemble Elateridae in the form of the prothorax and in the possession of a clicking device involving the prosternal process and mesosternal cavity, but they differ from all elaterids in having the labrum concealed beneath the clypeus, all 5 ventrites connate, and the antennae sometimes received in grooves just beneath the lateral pronotal carinae or ventrally crossing or bordering the notosternal suture. The tarsi are usually simple, but in *Galbites* they bear membranous appendages on segments 2–4. Larvae usually flattened, with no legs and reduced head with minute antennae and non-opposable or immovable mandibles. There are two common larval types: that found in *Fornax* and its relatives, in which the body is parallel-sided with a sclerotised, wedge-like head, and another, characteristic of *Trigonopleurus* and related groups, which resembles a buprestid larva in having an enlarged prothorax bearing rod-like sclerotisations. Most larvae occur in dead wood, but their food source and the mechanics of their locomotion through this substrate are still matters for speculation. They are liquid feeders and there is no evidence that they are predators; it is possible that they digest wood fibres extraorally, but they may also feed on slime mould plasmodium or some other nutrient-rich fluid within the wood. Larvae of the exotic *Phyllocerus* live in soil (Gur'yeva and Valiakhmedov 1982), and it is possible that some Australian species have the same habit. *Hemiopsida* is probably the largest Australian genus, and *Galbites* is a distinctive Melanesian genus which extends to Cape York. [Cobos 1964; J. C. M. Gardner 1935; Mamaev 1976a; Muona 1987]

**44. Throscidae** (Trixagidae; Fig. 35.38G). ADULT: ANT 11(MONR/3), FCOX GLOB(CONC), FCAV OPEN(OPEN), MCOX MWIDE–VWIDE(OPEN), 5-5-5, ABD 5(5), 1.6–3.5 MM. LARVA: HEAD PRO(PRO), STEM 0, ANT 2/3, FSUT 0, LABR FU, MOLA 0, VMP RET, MALA, MP 3, LP 2, HSC 0, HRD 0, VER 0, LEGS 5, TS 2, UROG +, SPIR BI.

Oblong to elongate, slightly flattened or rarely subcylindrical, pubescent beetles, with visible labrum, acute posterior pronotal angles, which fit closely against elytral humeri, 5 connate ventrites and tarsi without membranous appendages (although segment 4 is usually lobed below). Antennae usually with distinct 3-segmented club, but rarely moniliform with compact, subcylindrical segments. Like the Elateridae and Eucnemidae, throscids are able to jump by means of a clicking mechanism involving the

prosternal process and mesosternal cavity. Larvae lightly sclerotised and grub-like, with small head and reduced legs. Antennae very short; mandibles flattened, rounded and fused to head; prothorax with supporting rods; T9 with pair of minute, fixed urogomphi. The biology of Australian throscids is unknown, but larvae of the European *Trixagus dermestoides* feed in the soil on ectomycorrhizal fungi on the roots of various trees, and North American throscid larvae have been collected in rotten wood and grass tufts. The family, defined here in the narrowest sense (see Elateridae), is represented in Australia by *Trixagus*, *Aulonothroscus* and *Potergus*. [Burakowski 1975; Cobos 1961, 1966; Crowson 1961b; Lawrence 1982]

**45. Elateridae** (Figs 35.38E, 39K, L; Plate 4, H). ADULT: ANT 11(FIL/SERR/PECT/FLAB/INCR/4R), FCOX GLOB(CONC), FCAV OPEN(OPEN), MCOX MWIDE–VWIDE(OPEN–CLOS), 5-5-5, ABD 5(3R–4), 2.5–60 (4–45) MM. LARVA: HEAD PRO(PRO), STEM 0/1, ANT 3, FSUT 0, LABR FU, MOLA 0, VMP RET, MALA/GLAC, MP 3/4, LP 2, HSC 0/+, HRD 0, VER +, LEGS 5, TS 0R/2, UROG +/0, SPIR BI.

Beetles of characteristic elongate form, with acute hind angles on prothorax and a clicking mechanism enabling them to jump by forcing the long prosternal process suddenly into a cavity on the mesosternum causing a sudden movement of the prothorax relative to the hind body (M. E. G. Evans 1972, 1973). Labrum always visible; frontal area usually with sharp transverse ridge between eyes; antennae almost always serrate; tarsi simple or provided with setal brushes or membranous appendages; 5th ventrite more or less free, so that membrane usually visible between it and ventrite 4. Larvae elongate and cylindrical to slightly flattened, and either uniformly sclerotised and yellow to brown in colour, or more lightly sclerotised, except for head capsule, protergum and T9. Labrum and clypeus solidly fused to remainder of head capsule forming nasale, which is variously lobed or toothed; stemmata often reduced or absent; ventral mouth-parts consolidated to form maxillolabial complex; 10th segment reduced and ventrally situated; T9 terminal, with characteristic modifications (cylindrical, acute, forming concave plate or with simple or bifurcate urogomphi) in different genera.

Elaterid larvae (Figs 35.39K, L) may be saprophagous, feeding in rotten wood; phytophagous, feeding mainly on roots of plants; or predacious. In all cases, however, they are liquid feeding and practise extraoral digestion. Phytophagous larvae known as wireworms are pests of cereals, grasses and root crops. Species of *Pseudotetralobus* include the largest of Australian elaterids, and their larvae, which live in termite nests, are grub-like and densely clothed with long hairs. AGRYPNINAE include the common genera *Agrypnus* and *Conoderus*, which have soil-inhabiting larvae, as well as *Paracalais*, which is a predator of wood-boring beetles; *Agrypnus variabilis* is a major pest of sugar cane in Qld. Australian ATHOINAE include the genera *Hapatesus*, *Elatichrosis* and *Glypheus*, as well as the large Bassian genus *Crepidomenus* and its allies (Calder 1986). Common genera of ELATERINAE



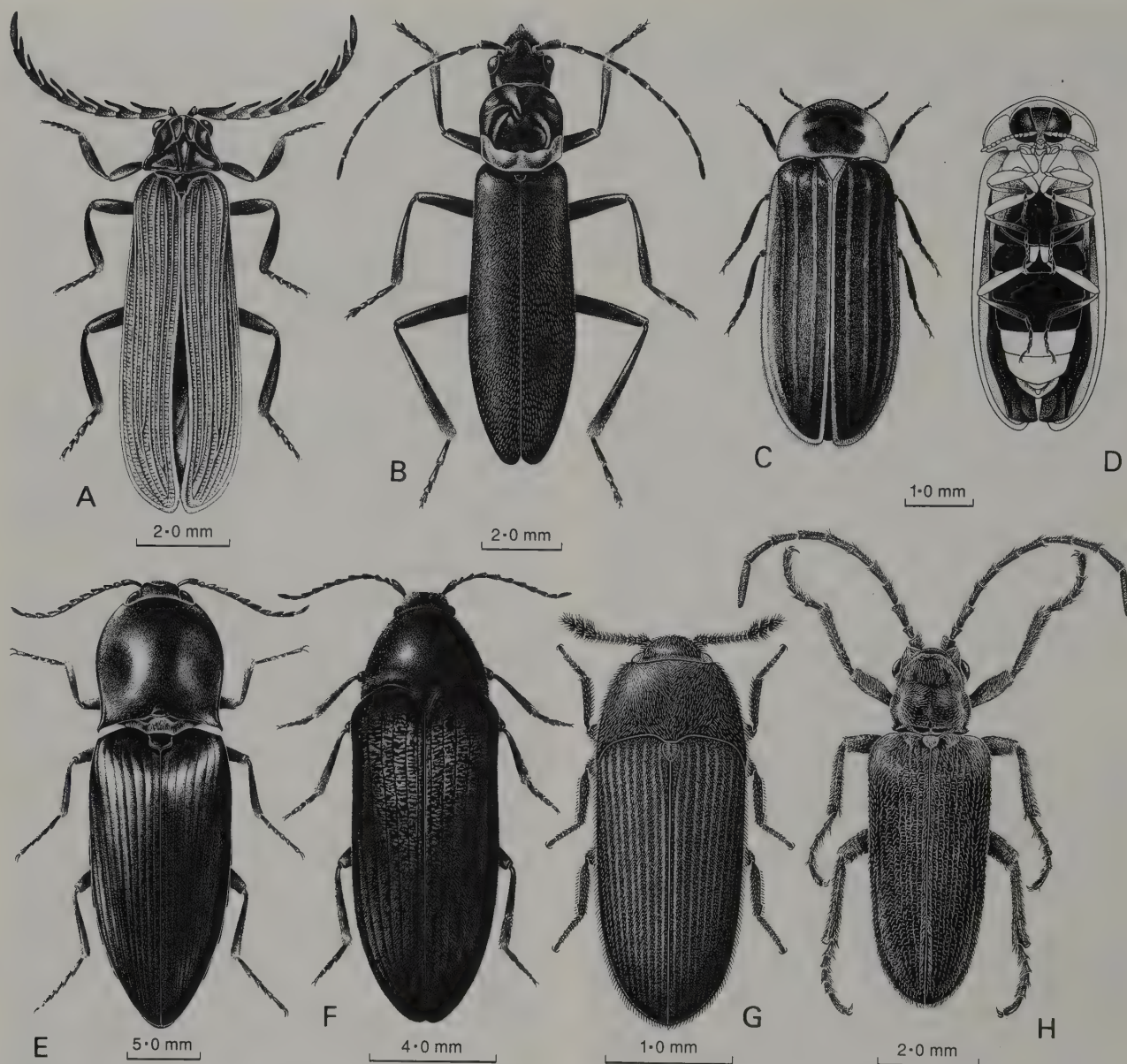


Fig. 35.38 Elateroidea: A, *Metriorrhynchus rhipidius*, Lycidae; B, *Chauliognathus lugubris*, Cantharidae; C, *Luciola lychnus*, Lampyridae, dorsal; D, same, ventral; E, *Lanelater mastersi*, Elateridae; F, *Euryptychus porosus*, Eucnemidae; G, *Aulonothroscus* sp., Throscidae; H, *Rhinorhipus tamborinensis*, Rhinorhipidae. [A–F by F. Nanninga; G by S. P. Kim; H after Lawrence 1988b]

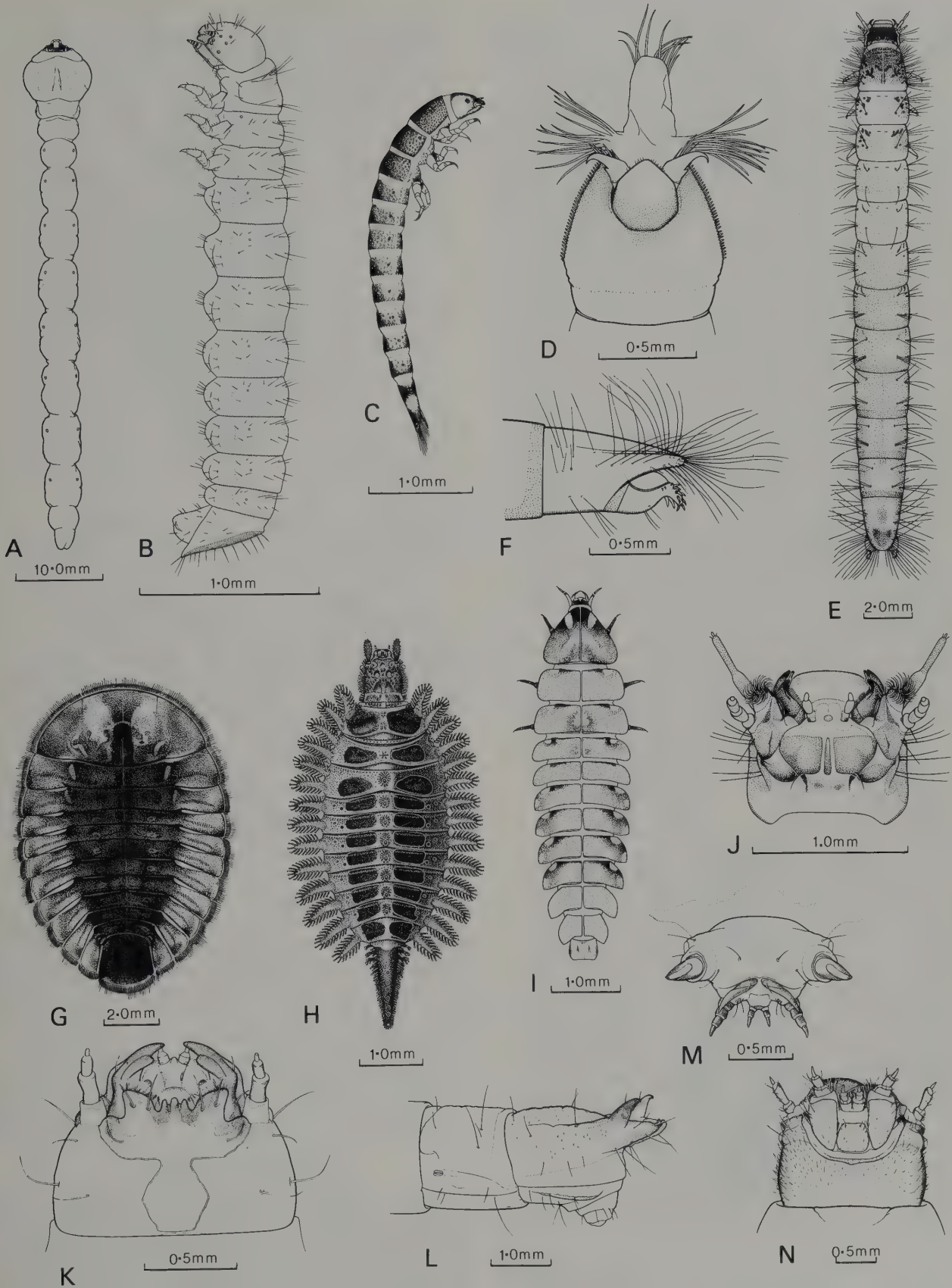
include *Anilicus*, *Glyphochilus*, *Dicteniophorus* and *Melanoxanthus*. *Paracardiophorus* (CARDIOPHORINAE) are abundant, and their unusual, slender larvae are predators in soil. Two groups often included in the family Throscidae but indistinguishable from elaterids on the basis of larval features are the THYLACOSTERNINAE and LISSOMINAE. The former are represented in North Qld by *Cussolenis mutabilis*, a cylindrical, eucnemid-like beetle with flabellate antennae, and the latter include *Drapetes*

and *Lissomus*, which are throscid-like in form, with long membranous lobes on the tarsi and antennae enclosed in deep cavities beneath the prothoracic hypomera. [Burakowski 1973; Crowson 1961b; Eidt 1959; Gur'yeva 1969; Lawrence 1988b; McDougall 1934; Neboiss 1956, 1961, 1967; Stibick 1979]

**46. Lycidae** (Figs 35.38A, 39M; Plate 6, A). ADULT: ANT 11(FIL/SERR/PECT/FLAB), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX CONT-NARR(OPEN), 5-

Fig. 35.39 Elateriform larvae: A, Buprestidae, dorsal; B, *Microchaetes* sp., Byrrhidae, lateral; C, *Austrolimnius waterhousei*, Elmidae, lateral; D, *Notriolus* sp., Elmidae, abdominal apex, ventral, showing operculum, hooks and extruded gills; E, *Byrrhocryptus* sp., Ptilodactylidae, dorsal; F, same, abdominal apex, lateral; G, *Sclerocyphon* sp., Psephenidae; H, *Brachypsectra* sp., Brachypsectridae; I, *Luciola* sp., Lampyridae; J, *Byrrhocryptus* sp., head, ventral, showing divided postmentum; K, *Hapatesus hirtus*, Elateridae, head, dorsal; L, same, abdominal apex, lateral; M, *Metriorrhynchus rhipidius*, Lycidae, head, anterodorsal; N, *Chauliognathus lugubris*, Cantharidae, head, ventral. [A, D, J–N by A. Klinkenberg; B, H by S. P. Kim; C, E–G, I by F. Nanninga]





5-5, ABD 7-8(0), 4.5-20 mm. LARVA: HEAD PRO (PRO/RET), STEM 1, ANT 2, FSUT 0, LABR FU, MOLA 0, VMP RET, MALA, MP 4, LP 2, HSC 0, HRD +, VER 0, LEGS 5, TS 2, UROG 0/+R, SPIR BI.

Elongate beetles with soft integument, flattened form, narrow, dehiscent elytra, which usually have longitudinal ridges or rows of window punctures, and aposematic coloration involving various combinations of reddish yellow and black. Head triangular or rostrate and partly covered by pronotum; antennae long, thick and approximate or contiguous; eyes well separated; maxillary palps expanded apically; pronotum usually with surface divided by ridges into cell-like compartments; femora and tibiae flattened; tarsal segments, especially 3 and 4, lobed beneath. Larvae elongate and somewhat flattened, usually heavily sclerotised and sometimes tuberculate. Head small with non-opposable, blade-like mandibles, which are longitudinally divided into 2 parts (Figs 35.16Q, 39M); segment 10 small and ventrally situated. Adult lycids are usually found on plant surfaces or in blossoms, where they probably feed on nectar or not at all. They are distasteful to birds and form part of mimicry complexes which also include beetles in the families Buprestidae, Meloidae, Pythidae, Oedemeridae, Cerambycidae and Belidae (Plate 6, B-E), as well as moths, flies and wasps. Lycid larvae occur beneath bark or in leaf litter and soil, and they are thought to feed on soft, decaying plant material or possibly slime mould plasmodia or yeasts. The commonest Australian genera are *Metriorrhynchus*, *Trichalus* and *Xylobanus*. [Crowson 1972b; Lea 1909]

**47. Lampyridae** (fireflies; Figs 35.38C, D, 39I). ADULT: ANT 11(FIL), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX CONT(OPEN), 5-5-5, ABD 6(0), 3.8-12 mm. LARVA: HEAD PRO(RET), STEM 1, ANT 3, FSUT 0, LABR FU, MOLA 0, VMP RET, MALA, MP 3/4, LP 2, HSC 0, HRD +, VER 0/+, LEGS 5, TS 2, UROG 0, SPIR BI.

Elongate, somewhat flattened, soft-bodied beetles with very large eyes in male and with luminous organs (yellowish white in colour) on 5th (female) or 5th and 6th (male) ventrites. Head concealed by the explanate pronotum or partly exposed; antennae relatively short; mandibles small, curved, falcate and perforate; 4th tarsal segment bilobed; colour of pronotum primarily yellow, elytra dark brown, usually with basal, lateral and sutural edges yellow. In most species the elytra are simple and complete, but in some females they may be shortened, and in *Pteroptyx* males they are apically deflexed. Larvae (Fig. 35.39I) elongate, tapered at both ends, somewhat flattened, dorsally sclerotised and variously marked, with small, retractable head bearing curved, perforate mandibles, and often with laterally expanded thoracic and abdominal terga. There is a luminous organ on segment 8, 9 is terminal, and 10 is reduced and bears a holdfast organ consisting of several eversible, asperate, tubular filaments.

The Australian lampyrid fauna is relatively poor, consisting of several species of *Luciola* (including *Atyphella*), *Pteroptyx cribellata* and a *Pyrophanes* from North Qld. Lampyrids are restricted to the wetter areas

along the eastern coast and are usually found in rain-forests and mangrove flats. Males fly just after dusk and emit a series of controlled flashes from the light organs as part of the mating sequence; females also flash but have not been observed to fly with the males. Synchronised flashing, well known in some New Guinea species, has been observed in North Qld. Adults are not known to feed, but larvae prey on small land snails, which they paralyse using secretions produced by a pair of acinose glands at the anterior end of the alimentary canal and injected through the perforate mandibles; the prey is digested extraorally and the liquefied tissues are imbibed. Larvae and pupae are also faintly luminous; the possible adaptive significance of larval luminescence has been discussed by Sivinski (1981). [Ballantyne 1968, 1987a, 1987b; Ballantyne and McLean 1970; Crowson 1972b]

**48. Cantharidae** (Figs 35.38B, 39N). ADULT: ANT 11(FIL), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX CONT(OPEN), 5-5-5, ABD 7-8(0), 2.5-15 mm. LARVA: HEAD PRO(PRO), STEM 1, ANT 3, FSUT 0, LABR FU, MOLA 0, VMP RET/PRO, MALA, MP 3/4, LP 2, HSC 0, HRD 0, VER +, LEGS 5, TS 2, UROG 0, SPIR AN/CR.

Elongate, parallel-sided, soft-bodied beetles usually in various combinations of yellow and black or bluish black. Head relatively large and deflexed; labrum membranous and often inconspicuous; antennal insertions well separated; pronotum oval or subquadrate and flattened; 4th tarsal segment bilobed; male genitalia usually large, asymmetrical and exposed. The elytra are usually complete, but they are abbreviated in *Chauliognathus apterus* from Lord Howe I. Larvae elongate and lightly sclerotised (although often darkly pigmented or patterned), with characteristic clothing of fine, velvety pile. Stemmata well developed (Fig. 35.39N); mandibles more or less falcate; gular region well developed, without or with fused sutures; paired glandular openings on all thoracic and abdominal segments; segment 10 reduced and terminal. Adult cantharids are active during daylight and are sometimes found in large numbers on flowers and vegetation. They are known to attack other insects, but they may feed as well on pollen, nectar and fresh foliage. Like the Lycidae, they produce defensive chemicals and belong to mimicry complexes. Larvae are common in soil and leaf litter, where they are usually general predators; some Holarctic species, however, are known to be phytophagous. Australian species belong to the genera *Chauliognathus*, *Heteromastix* and *Sphaerarthrum*, and a particularly common species in the south-east is the greyish-green and orange *C. lugubris*. [Brancucci 1980; Crowson 1972b; Lea 1909]

### Series BOSTRICHIFORMIA

This is a paraphyletic assemblage including those Polyphaga which appear to belong to the cucujiform lineage (Crowson 1960; Lawrence and Newton 1982) but lack the apomorphic features of the series Cucujiformia. Relationships among the included taxa are not well understood. The first four families were placed by Crowson (1959, 1960) in a superfamily Dermestoidea.





Fig. 35.40 *Nothoderodontus darlingtoni*, Derodontidae.  
[S. P. Kim; after Lawrence 1985a with permission of Kluwer Academic Publishers]

### Superfamily DERODONTOIDEA

**49. Derodontidae** (Fig. 35.40). ADULT: ANT 11(3), FCOX PROJ(CONC), FCAV CLOS(OPEN), MCOX NARR(OPEN), 5-5-5, ABD 5(0), 1.7-2.1 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, GLAC, MP 3, LP 2, HSC +, HRD 0, VER +, LEGS 5, TS 2, UROG +, SPIR AB.

Distinctive beetles with paired ocelli and a series of canals and bridges on head, pronotum divided into several cells by longitudinal ridges and transverse elevations, and elytra with a number of deep pits at bases of striae. Mid coxal cavities partly closed by metepisterna; metasternum with transverse suture; hind coxal plates well developed; a pair of longitudinal carinae near middle of ventrite 1. Larvae elongate, slightly tapered posteriorly, with dorsal surfaces granulate, tuberculate and usually with paired processes on all segments except 10th, which is cylindrical and posteroventrally oriented. Head transverse, with no epicranial stem and contiguous frontal arms, and spiracles borne on tubular processes. The only Australian species is *Nothoderodontus darlingtoni*, which occurs in wet forest in Tas., Vic. and the A.C.T. Its habits are unknown, but the New Zealand *N. gourlayi* feeds on the hyphae and conidia of sooty moulds (Ascomycetes: Capnodiaceae and related families). [Lawrence 1985a]

### Superfamily BOSTRICOIDEA

Lawrence and Newton (1982) united Dermestidae with Bostrichoidea on the basis of modified cryptonephridism (Saini 1964), aedeagal structure and lack of a basal mandibular mola in the larva, and Ivie (1985) added Nosodendridae as well, assuming a secondary loss of cryptonephridism in both *Nosodendron* and the exotic

dermestid genus *Orphilus*. Caveney (1986) pointed out that both *Nosodendron* and *Dermestes* have exocone eyes, as in Endecatomidae, Bostrichidae and Anobiidae, whereas *Orphilus* and most Dermestidae have acone eyes. The position of Jacobsoniidae is questionable. Lawrence and Newton included it in Derodontoidea, Ivie (1985) proposed a new superfamily at the base of the Cucujiformia, and Sen Gupta (1979) placed the jacobsoniid subfamily Derolathrinae in the cucujoid family Merophysiidae (= Endomychidae). Although the condition of the Malpighian tubules in Jacobsoniidae has not been examined, the presence of fused rhabdomes in *Saphophagus* (Caveney 1986) does not support the inclusion of the group in Cucujiformia. The aedeagus in jacobsoniids is highly modified, with the tubular tegmen enclosing the penis, but there appears to be a basal connection between the two structures reminiscent of the condition in Bostrichoidea, where the family is tentatively placed.

**50. Jacobsoniidae** (Sarthriidae; Fig. 35.41). ADULT: ANT 10/11(MON/1-3), FCOX GLOB-PROJ(CONC), FCAV OPEN-CLOS(OPEN), MCOX NARR-MWIDE (CLOS), 3-3-3, ABD 5(0), 0.7-2.1 mm. LARVA: HEAD PRO(PRO), STEM 0, ANT 3, FSUT +, LABR FR, MOLA +, VMP RET, GLAC/MALA, MP 3, LP 2, HSC +, HRD 0, VER 0, LEGS 5, TS 1, UROG +, SPIR AN.

Narrowly elongate beetles with metasternum as long as or longer than all 5 ventrites combined, maxillary palps aciculate, and basal tarsal segments reduced, so that tarsi may appear 2-segmented. Larvae elongate, slightly flattened, and sclerotised dorsally, with short antennae and short, fixed urogomphi. The Australian fauna includes *Sarthrias lawrencei* from North Qld and several undescribed Derolathrinae. The former (Fig. 35.41) is a



Fig. 35.41 *Sarthrias lawrencei*, Jacobsoniidae.  
[A. Hastings; after Löbl and Burckhardt 1988]

distinctive looking beetle with scale-like setae on the antennae and tracts of silvery tomentum covering much of the body surface. Derolathrines are minute (less than 1 mm) and yellowish brown, with the head abruptly constricted behind the eyes to form short temples and the antennae 10- or 11-segmented with a 1- or 2-segmented club. Derolathrines have been seen from Norfolk I., Lord Howe I., Christmas I. and various parts of Qld, the A.C.T. and S.A. [Löbl and Burkhardt 1988; Sen Gupta 1979; Ślipiński 1986]

**51. Nosodendridae** (Figs 35.42A, B). ADULT: ANT 11(3), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX MWIDE-VWIDE(OPEN), 5-5-5, ABD 5(0), 3.7-5.5 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT +, LABR FR, MOLA +, VMP RET, GLAC, MP 3, LP 2, HSC +, HRD 0, VER +, LEGS 5, TS 2, UROG 0, SPIR AB.

Ovoid, convex, glabrous and shining, black beetles, capable of folding their legs into ventral cavities, as in Byrrhidae. Unlike Byrrhidae, having prognathous head, well-marked, 3-segmented, tomentose antennal club, and maxillae and prementum concealed beneath enlarged mentum. Larvae elongate, fusiform, somewhat flattened, and dorsally granulate and tuberculate, with T8 forming tapered, terminal process with spiracles at apex. Frontal arms distant at base; 3rd antennal segment reduced; mandibles with complex armature and vestiture; maxillae provided with comb-hairs. At least 3 species of *Nosodendron* occur in eastern Australia; both larvae and adults live in slime fluxes which develop in tree wounds. [Costa *et al.* 1986]

**52. Dermestidae** (Figs 35.42C, D, F, G). ADULT: ANT 9R/11(FILR/PECT/FLABR/1R/3-8), FCOX TRANS-PROJ(EXP-CONC), FCAV OPEN(OPEN-CLOS), MCOX CONT-MWIDE(OPEN), 5-5-5, ABD 5/7-8R(0/2), 1-10 mm. LARVA: HEAD HYPO, STEM 0/3-6, ANT 3, FSUT 0R/+ LABR FR, MOLA 0, VMP RET, GLAC, MP 3/4, LP 2, HSC 0/+R, HRD 0, VER 0, LEGS 5, TS 2, UROG 0/+, SPIR AN.

Oblong to broadly ovate beetles almost always with deflexed head and clothed with erect or decumbent hairs or scales, sometimes forming a pattern. Except for the Dermestinae, Thorictinae and *Trichelodes*, all dermestids have a median ocellus on the head. Larvae elongate and subcylindrical to ovate and fusiform, with distinct tergites, and densely clothed with long hairs, some of which may be barbed (*spicisetae*) or spear-headed (*hastisetae*), serving as a defence mechanism by detaching and entangling potential predators (Nutting and Spangler 1969). Lacinia terminating in sclerotised spur or spine; mandible usually with membranous lobe and setal brush at base of mesal surface; and the urogomphi absent, except in *Dermestes* (and the exotic Thorictinae and Orphilinae).

Dermestidae usually feed as larvae on dry material of animal origin, such as insect remains, dry carcasses, hair or feathers, and they may occur in the nests of mammals, birds or social insects. Adults of some dermestids (*Anthrenus*, *Trogoderma*) are commonly found on flowers and feed on nectar or pollen, but others feed on the larval food source or not at all. The family includes a number of

cosmopolitan stored product pests, such as *Dermestes* species (DERMESTINAE), which attack hides, furs and skins, as well as some foodstuffs, species of *Anthrenus* (ANTHRENINAE) and *Attagenus* (ATTAGENINAE), which may damage carpets, blankets or other woollen fabrics, and various dermestids, particularly *Anthrenus verbasci*, which damage dried insect specimens. Only *Trogoderma granarium* is known to feed normally on cereal products, but it has not yet become established in Australia. Two other introduced pests known to attack insect collections have been found in the A.C.T.: the parthenogenetic *Reesa vespulae*, which has also been introduced into New Zealand (Waller and Watt 1979), and the unusual *Thylotrias contractus* (THYLODRIINAE), females of which are larviform. Except for *Trichelodes delicatula* (TRINODINAE) and an undescribed trinodine from North Qld, all native dermestids belong to the large subfamily Anthreninae. Included are *Anthrenocerus australis*, which has been reported as a household pest, the myrmecophilous *Myrmeanthrenus frontalis*, and *Thaumaglossa nigricans*, which lives in mantid egg cases. [Armstrong 1945; Hinton 1945a; Mroczkowski 1968; Peacock 1978.]

**53. Bostrichidae** (Bostrychidae, incl. Lyctidae; Figs 35.42E, H). ADULT: ANT 9-11(2-3), FCOX GLOB-PROJ(CONC), FCAV OPEN-CLOS(CLOS), MCOX CONT-VWIDE(CLOS), 5-5-5, ABD 5(0), 2-20 mm. LARVA: HEAD PRO(RET), STEM 0, ANT 3, FSUT +, LABR FR, MOLA 0/PS, VMP RET, GLAC, MP 2/3, LP 1/2, HSC 0/+, HRD +, VER 0, LEGS 5, TS 0/2, UROG 0/+R, SPIR AN.

Elongate, cylindrical to slightly flattened, black or brown beetles, with head prognathous and visible from above (Lyctinae) or strongly deflexed and concealed from above by prothorax (Dinoderinae and Bostrichinae). Antennal club usually relatively loose; eyes circular and strongly projecting laterally; lateral pronotal carinae weak or absent; hind coxae contiguous to widely separated, without coxal plates; tarsi relatively slender and not lobed beneath. In the more cylindrical, burrowing forms, the head, pronotum and elytral apices may be tuberculate, toothed or otherwise modified, and the fore tibiae may be dentate; these resemble scolytine weevils, which differ in having geniculate antennae with a more compact club, elongate, less protruding eyes, and lobed tarsi with a reduced 4th segment. Larvae C-shaped and very lightly sclerotised, with enlarged thoracic region and strongly retracted head. Most bostrichids bore into moribund or freshly felled trees, dead and dry sapwood, or other kinds of dry plant material containing starches and sugars. They cannot produce cellulases and thus are restricted to sapwood, which the larvae reduce to a soft powder, earning them the name powderpost beetles.

There are three major introduced pest species in Australia: *Lyctus brunneus*, which attacks structural timber containing sapwood; *Dinoderus minutus* (DINODERINAE), which commonly infests bamboos, cane furniture or basketwork; and *Rhyzopertha dominica* (Dinoderinae), which is our most serious pest of stored grain. The native bostrichid fauna includes several LYCTINAE (*Lyctus*, *Lyctodon*, *Trogoxylon*, *Tristaria*,



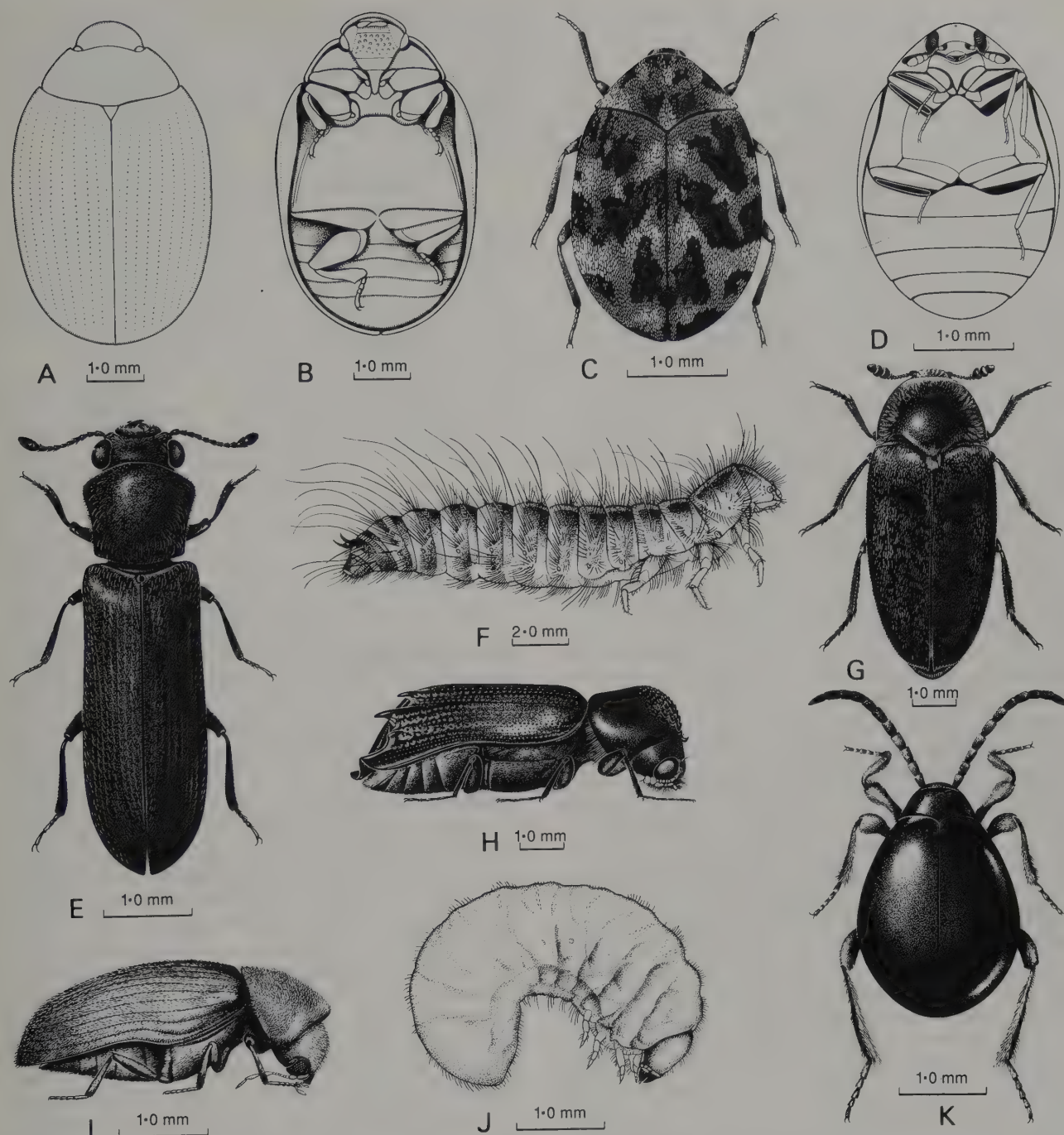


Fig. 35.42 Bostrichoidea: A, *Nosodendron australicum*, Nosodendridae, dorsal; B, same, ventral; C, *Anthrenus verbasci*, Dermestidae-Anthreninae, dorsal; D, same, ventral; E, *Lyctus brunneus*, Bostrichidae-Lyctinae; F, *Dermestes maculatus*, Dermestidae-Dermestinae, larva; G, same, adult; H, *Xylion cylindricus*, Bostrichidae-Bostrichinae; I, *Stegobium paniceum*, Anobiidae-Anobiinae, adult; J, same, larva; K, *Gibbium psyllodes*, Anobiidae-Ptininae. [F. Nanninga]

*Minthea acanthacollis*) and a large number of BOSTRICHINAE. Our largest species is *Bostrychopsis jesuita*, which is widely distributed across the northern part of the continent and normally attacks wattles and eucalypts. *Xylion*, *Xylobosca*, *Xylopsocus* and related genera contain most of our smaller species, many of which have concave elytral apices with which the males block the tunnel entrances against predators and parasitoids while the female is laying eggs. In *Xylobosca bispinosa* the

males have, in addition to the concave declivity, a pair of diverging spines, which are lacking in the female. [Crowson 1961a; Lawrence 1980; Vrydagh 1958]

**54. Anobiidae** (incl. Ptinidae, Ectrephidae; Figs 35.42I–K). ADULT: ANT 3R/6 10R/11(FIL/SERR/PECT/FLABR/1–2R/3), FCOX GLOB–PROJ(EXP–CONC), FCAV OPEN(CLOS), MCOX MWIDE–VWIDE(CLOS), 5–5–5, ABD 5(2–3), 1.1–8.5 mm. LARVA: HEAD HYPO, STEM 0/1, ANT 1/2, FSUT +, LABR FR,

MOLA 0/PSr, VMP RET, GLAC, MP 3/4, LP 2, HSC 0/+R, HRD 0, VER 0, LEGS 0R/5, TS 2/M, UROG 0, SPIR AN/AU.

Convex, elongate and cylindrical to ovate and globose beetles, variously clothed with decumbent or erect hairs or scales and only occasionally glabrous above. Head strongly deflexed and usually concealed from above; prosternum reduced and sometimes deeply excavate forming a cavity which continues on mesosternum; trochanters squarely attached to bases of femora; antennae variable, but usually filiform, serrate, or with large, loose, elongate club. Hind coxae usually contiguous and excavate to receive femora (with coxal plates), except in Ptininae, where they are widely separated and non-excavate (lacking coxal plate); most ptinines also have approximate antennal insertions and no lateral pronotal carinae, but this is not the case in the genus *Neoptinus*. Larvae C-shaped and very lightly sclerotised, with exserted, hypognathous head, very small antennae, and pair of oval lobes on segment 10 beneath anus.

Most larval Anobiidae bore into the wood or bark of dead trees, and a few have become pests of furniture or timber in Australia. The most serious pest is the furniture beetle, *Anobium punctatum* (ANOBIINAE). The introduced *Ernobius mollis* attacks pine timber which still has some bark attached. The native species *Calymmaderus incisus* attacks softwoods but has also been reported from *Eucalyptus* wood (Hockey 1986). Most species of *Dryophilodes*, our largest genus, feed on the woody fruits of *Eucalyptus* and other Myrtaceae (Andersen and New 1987), but at least one is known to attack *Araucaria* seed cones. Two cosmopolitan species, *Stegobium paniceum* and *Lasioderma serricorne*, are important stored product pests, while some members of the DORCATOMINAE feed on woody or fibrous fungal fruiting bodies. Members of the PTININAE feed mainly on dry materials of animal or plant origin and are common inhabitants of the nests of birds, mammals and social insects. *Ptinus exulans* lives on the arthropod remains in spider nests (Hickman 1974), while several introduced species, such as *Mezium americanum*, *M. affine*, *Gibbium aequinoctiale* and *Ptinus tectus*, are stored product pests. A large number of ptinines in the genera *Diplocotes*, *Polyplocotes*, *Enasiba* and *Ectrephes* are specialised symphiles in the nests of ants, especially those of *Iridomyrmex* species (Lawrence and Reichardt 1969). [Bellés 1985; Bellés and Lawrence 1984, 1990; Español 1976, 1977, 1979; Ford 1970; Hinton 1941; Lea 1924; R. E. White 1974]

### Series CUCUJIFORMIA

The monophyly of this group appears to be well founded, being based on a number of adult features, such as the presence of acone eyes with open rhabdomes (Caveney 1986), cryptonephridial Malpighian tubules of the 'normal' type (pp. 556, 641), absence of plates on the hind coxae, absence of functional spiracles on abdominal segment 8, reduction of the pregenital segments (9 and 10) and the presence of a hylecoetoid type of metendosternite (p. 547) and cucujoid type of aedeagus (p. 552) or their derivatives. Larvae retain most of the primitive polypha-

gan features, but usually have the galea and lacinia fused to form a single mala. Of the six included superfamilies, there is little doubt about the monophyly of Lymexyloidea, Chrysomeloidea and Curculionoidea, but the limits of and relationships among the remaining three are far from clear.

### Superfamily LYMEXYLOIDEA

This group represents an isolated lineage in which the specialised, wood-boring larva retains a separate galea and lacinia and the aedeagus somewhat resembles that found in Bostrichoidea. Crowson (1981) placed the Strepsiptera (see Chapter 36) in this superfamily on the basis of relatively weak evidence reviewed by Lawrence and Newton (1982) and Wheeler (1986).

**55. Lymexylidae** (Fig. 35.43). ADULT: ANT 11 (SERR/PECT/INCR), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX CONT(OPEN), 5-5-5, ABD 5-7(0), 7.5-35 mm. LARVA: HEAD HYPO, STEM 0/5/6, ANT 3, FSUT 0/+, LABR FR, MOLA +, VMP RET, GLAC/MALA, MP 3, LP 2, HSC +, HRD 0/+, VER +, LEGS 5, TS 2/M, UROG 0, SPIR AN/AM.

Very long and narrow, finely pubescent beetles with well-developed eyes, sometimes very large and dorsally contiguous. Legs long with projecting coxae; metepisterna meeting at midline; elytra rounded apically and exposing abdominal apex or (*Atractocerus*) most of abdomen and hind wings, which lack transverse folds. A branched sensory organ arises from the 3rd maxillary palp segment in males of *Melittomma* and males and females of *Atractocerus*. Larvae very long, narrow and cylindrical, with globular head, very short antennae, enlarged and dorsally humped prothorax, and terminal T9, which forms lightly sclerotised, rounded and asperate protuberance (*Atractocerus*) or heavily sclerotised, concave plate lined with teeth. Lymexylid larvae bore into hard wood of weakened or dead trees and feed on ambrosia fungi of the genus *Ascoidea* (Ascomycetes: Endomycetales), which grows on their tunnel walls. Adult females carry the fungal spores in pouches near the end of the ovipositor and deposit them in a slimy matrix with the eggs. The 1st instar larvae then transport the spores into the wood on their bodies (Francke-Grosmann 1967). In Australia lymexylids damage commercial timber because of the darkly stained 'pinholes' they form within the wood. In addition to *Atractocerus* and *Melittomma*, which are distributed throughout the tropical regions of the world, the Australian fauna includes the endemic genus *Australymexylon*. [J. Clark 1925; Wheeler 1986]

### Superfamily CLEROIDEA

Although some basal members of this group are difficult to distinguish from Cucujoidea, most cleroids have a distinctive adult habitus, with projecting fore coxae and 5 (often lobed) tarsal segments, and larvae have only 1 tarsal seta, no mandibular mola, and usually a pedunculate seta on the mala. Although phloiophilids and some trogossitids are mycophagous, most other cleroids are predacious in all stages or predacious as larvae and pollen-feeding as adults. Exotic families include the



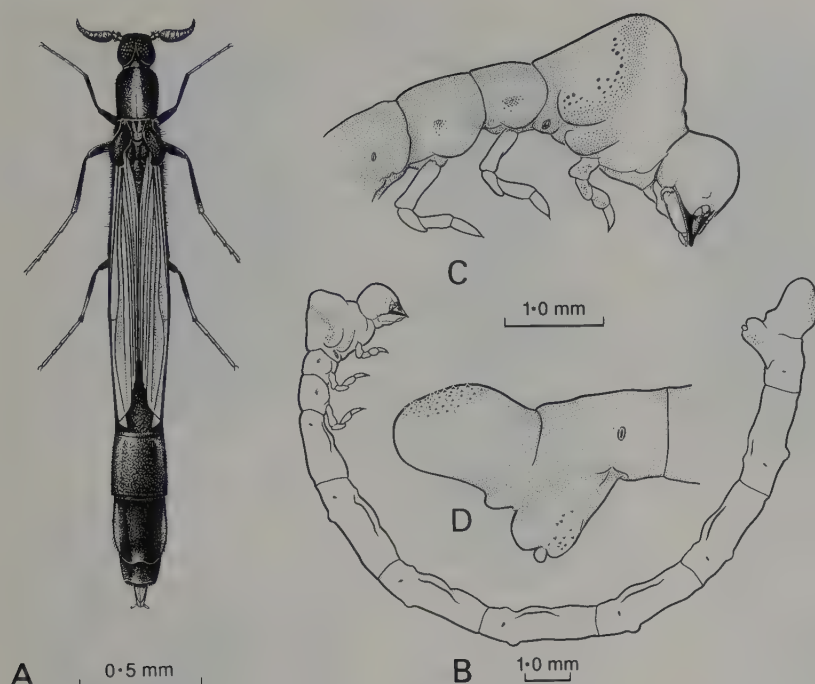


Fig. 35.43 Lymexylinidae: A, *Atractocerus crassicornis*; B, *Atractocerus* sp., larva, lateral; C, same, head and thorax, lateral; D, same, abdominal apex, lateral.

[A by F. Nanninga; B–D by S. Smith]

Palearctic Phloiophilidae and the Chaetosomatidae from New Zealand and Madagascar.

**56. Trogossitidae** (incl. Peltidae, Lophocateridae; Figs 35.44B–E). ADULT: ANT  $7R/9-11(1-2R/3)$ , FCOX TRANS/PROJR(EXP), FCAV OPEN-CLOS(OPEN-CLOS), MCOX CONT-MWIDE(OPEN-CLOS), 5-5-5, ABD 5(0), 1-18 (3-15) MM. LARVA: HEAD PRO(PRO), STEM 2-5, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP RET, MALA, MP  $2R/3$ , LP  $1R/2$ , HSC 0, HRD +, VER 0/+, LEGS 5, TS 1, UROG +, SPIR AB.

The family, as here constituted, was divided by Crowson (1970) into three separate families and includes several subgroups with very different looking adults. Most species are ovate to elongate and more or less flattened, with a prognathous head, short antennae bearing a large, loose, slightly asymmetrical, 3-segmented club, and a vestiture of short or long hairs, bristles or scales. *Larinotus*, however, is strongly convex with a deflexed head; *Egolia* is subcylindrical and glabrous; all members of the EGOLIINAE have a 1- or 2-segmented, compact antennal club; and RENTONIINAE are minute, globose and clambid-like. Although the tarsi are always 5-segmented, the first segment may be reduced and partly concealed by the tibial apex. Subovate, flattened trogossitids, like *Ancyrona laticeps*, are similar to some Nitidulidae, but in the latter the antennal club is much smaller and more compact. Larvae elongate, parallel sided, slightly to strongly flattened, and lightly sclerotised, except for head and usually additional sclerites on thorax and T9; mandible usually with 1 or several hyaline processes at base of mesal edge; ventral mouth-parts consolidated, without articulating areas; hypostomal rods usually long and parallel; *para-gular* sclerites usually present between gula and hypostomal rods; urogomphi well developed in most species but minute in *Larinotus*. Most Trogossitidae are predacious as larvae and adults, but *Larinotus umbili-*

*catus* feeds on fungus fruiting bodies and some LOPHOCATERINAE may also be mycophagous. Most trogossitids are found under bark, but Rentoniinae are usually collected in leaf litter. Species of *Lepidopteryx* (*Leperina*) (TROGOSSITINAE), our most common genus, are clothed with scales or bristles forming a pattern. The introduced *Tenebroides mauritanicus* is a cosmopolitan stored product pest; although basically predacious, both adults and larvae will feed directly on grain and seeds. [Aitken 1975; Crowson 1964b, 1966a, 1970; Lawrence 1980; Mamaev 1976b]

**57. Cleridae** (Figs 35.44A, H). ADULT: ANT 11 (FIL/SERR/PECT/INCR/3-6), FCOX PROJ(EXP-CONC), FCAV OPEN-CLOS(OPEN), MCOX NARR (OPEN/CLOSr), 5-5-5/P4-4-4/4-4-4, ABD 5-6(0), 1.8-4.4 (5-25) MM. LARVA: HEAD PRO(PRO), STEM 0-6, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP PRO, MALA, MP 3, LP 2, HSC 0, HRD 0/+, VER 0/+, LEGS 5, TS 1, UROG 0/+, SPIR AN/AB.

Elongate, parallel-sided beetles, clothed with erect, or erect and decumbent hairs and often either metallic in colour or patterned with red or yellow. Head usually more or less deflexed; eyes usually slightly to strongly emarginate; antennae short; labial palps often enlarged and securiform; pronotum usually without lateral carinae; prosternum well developed in front of coxae; tarsi with one or more segments lobed or with membranous appendages; 1st tarsal segment sometimes reduced and concealed within tibial apex. Larvae elongate, cylindrical to somewhat flattened, and lightly sclerotised except for head, one or more tergal plates on thorax and T9 but cuticle often pigmented with yellow, pink, blue or brown. Head well sclerotised dorsally and ventrally; gula long and narrow; mandible with hyaline process at base; except in few Thaneroclerinae, epicranial stem absent and median endocarina present.

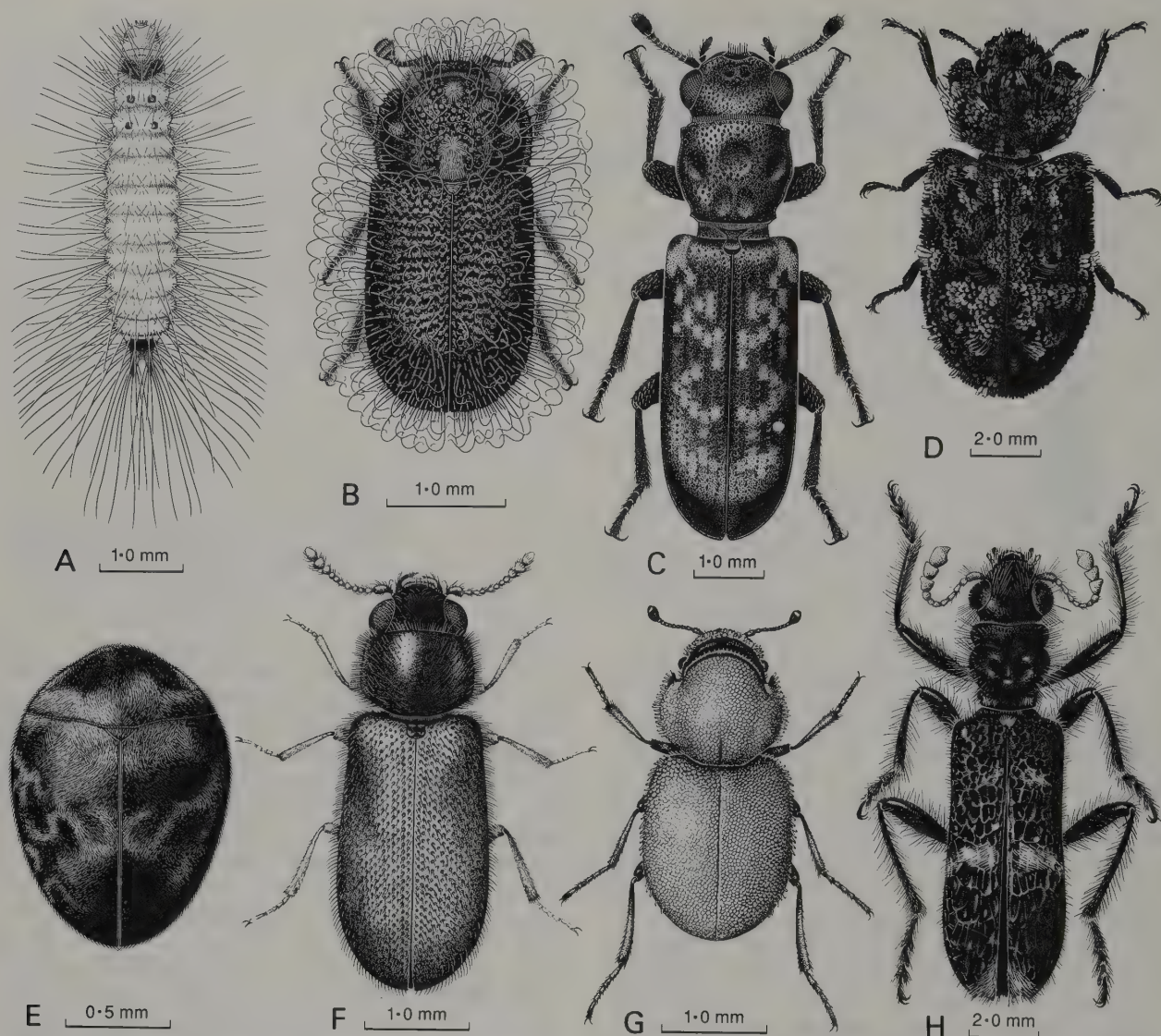


Fig. 35.44 Cleroidea: A, *Lemidia* sp., Cleridae, larva; B–E, Trogossitidae: B, *Larinotus umbilicatus*, Egoliinae; C, *Egoia variegata*, Egoliinae; D, *Lepidopteryx turbata*, Trogossitinae; E, *Parentonium* sp., Rentoniinae; F, *Acanthocnemus nigricans*, Acanthocnemidae; G, *Phycosecis littoralis*, Phycosecidae; H, *Scrobiger splendidus*, Cleridae. [A–C, E by S. P. Kim; D, F–H by F. Nanninga]

Both larvae and adults of almost all Cleridae prey upon other insects, especially those associated with bark or wood. Adults are very active and usually diurnal; they are often found on flowers, foliage and tree trunks. *Lemidia* species are relatively small and brightly coloured, with a narrow prothorax and large, protruding eyes; adults of *L. subaenea* have been observed feeding on psyllids (HEMI) on the surfaces of *Acacia* leaves (New 1978a), but *Lemidia* larvae are also the most common clerids in leaf litter. Little is known of the biology of our larger CLERINAE, such as *Eunatalis titana* and *Trogodendron fasciculatum*, but the latter is an important predator of wood-boring Cerambycidae. *Zenithicola crassus* is a predator in termite nests, and its larva is clothed with very long hairs like those of the termite-feeding elaterid larvae in the genus *Pseudotetralobus* (B. P. Moore 1973). The THANEROCLERINAE are usually very small inhabitants of fungal fruiting bodies, but *Thaneroclerus buquet* occurs

in stored products, where it is commonly associated with the anobiid *Lasioderma serricorne*. *Paratillus carus* and *Tarsostenus univittatus* (TARSOSTENINAE) and *Cylidrus* species (TILLINAE) invade the tunnels of various Bostrichidae and a few scolytine Curculionidae. The introduced *Necrobia ruficollis* and *N. rufipes* (KORYNETINAE) occur in carrion and in stored products of animal origin; the latter, however, is also common in copra cargoes, where it feeds directly on the copra, as well as on other insects. [Aitken 1975; Crowson 1964b; Froggatt 1927; Winkler 1982]

**58. Acanthocnemidae** (Fig. 35.44F). ADULT: ANT 11(3), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-5, ABD 5(0), 3.5–5.5 mm. LARVA: UNKNOWN.

Elongate, flattened, black beetles clothed with stiff, erect hairs and similar to dasytine Melyridae, from which they differ in having a distinct antennal club and pair of



unusual, partly covered, hypomerical cavities in front of fore coxae. A putative 1st instar larva described by Crowson (1970) has the characteristics of a trogossitid, but the association is doubtful. *Acanthocnemus nigricans* is widely distributed in Australia and has been introduced into New Caledonia and various parts of Europe, Asia and Africa. Adults may fly to lights at night and have been observed flying around a log dump and coming to the hot ashes of a campfire. [Champion 1922]

**59. Phycosecidae** (Fig. 35.44G). ADULT: ANT 10(1), FCOX TRANS(CONC), FCAV CLOS(OPEN), MCOX NARR(CLOS), 4-4-4, ABD 5(0), 1.6-3.4 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP RET, MALA, MP 3, LP 2, HSC 0, HRD +, VER 0, LEGS 5, TS 1, UROG +, SPIR AN.

Ovate, convex beetles, with prognathous head, partly covered by semicircular projection of anterior edge of pronotum, and dorsal vestiture of flattened, whitish scales. Anterior pronotal angles strongly produced forward; metasternum very short; hind wings absent. Larvae very similar to those of Melyridae, except for short epicranial stem and presence of 6 stemmata. The family includes one genus, *Phycosecis*, with species occurring among sand dunes along the coastlines of New Zealand and Australia. Larvae and adults are scavengers and have been found on dead birds and fishes. Crowson (1964b) found insect parts in the larval gut of the New Zealand *P. limbata*, but *P. litoralis* has been reared through an entire generation in a closed container with fish, lettuce and bran, and larvae were usually clustered beneath pieces of rotting fish. In Australia, *P. hilli* occurs in North Qld, *P. ammophila* is known from W.A., and *P. litoralis* is distributed from Dongara, W.A., along the coast of S.A. and Vic., north at least to Sydney, N.S.W. [Crowson 1964b]

**60. Melyridae** (Fig. 35.45). ADULT: ANT 10A-11(FIL/SERR/PECT/FLAB/INCR), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX CONT(OPEN), 5-5-5/4-5-5♂\*, ABD 6(0), 1-10 mm. LARVA: HEAD PRO(PRO), STEM 1-5, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP

RET, MALA, MP 3, LP 2, HCS 0, HRD 0, VER 0, LEGS 5, TS 1, UROG +, SPIR AN.

Oblong to elongate, somewhat flattened, soft-bodied beetles, usually clothed with decumbent hairs and scattered erect setae, and either uniformly black or grey (Dasytinae) or bicoloured with red or yellow and blue or black (Malachiinae). Labrum well sclerotised; tarsal claws toothed or provided with a pair of fleshy appendages; elytra sometimes very short, exposing several abdominal tergites; eversible vesicles often on prothorax, mesothorax and abdomen. Larvae elongate, slightly flattened, lightly sclerotised, except for head, T9 and thoracic plates, and red or pink in colour (like some clerid larvae); head with long epicranial stem, no median endocarina, and lightly sclerotised gular and para-gular areas, so that head capsule appears to be open behind ventral mouthparts; as in most cleroids, mesal appendage at base of mandible. Adult melyrids are often found on flowers and a number of them feed on pollen (Hawkeswood 1987b; Schicha 1974), but Crowson (1964b) found insect fragments in the guts of adults belonging to several species. Larvae are usually predacious, but may also be scavengers (Fiori 1971); larvae of *Dicranolaius villosus* are known to feed on locust egg pods (Farrow 1974a).

Only two subfamilies, DASYTINAE and Malachiinae, occur in Australia. Species in the former group have all been placed in the genus *Dasytes*, but they are not congeneric with members of that Palaearctic group (K. Majer 1987); most are small and grey or black, without obvious sexual dimorphism. The MALACHIINAE are common and abundant throughout the continent. The largest group have short elytra and are included in *Carphurus*, *Neocarphurus*, *Helcogaster* and *Balanophorus*; males of the first three and both males and females of the last have the first segment of the fore tarsus enlarged and provided with a fine black comb. Those malachiines with complete elytra have 11-segmented antennae (*Hypattalus*) or apparently 10-segmented antennae (with the pedicel reduced and concealed within the apex of the scape) (*Laius* and

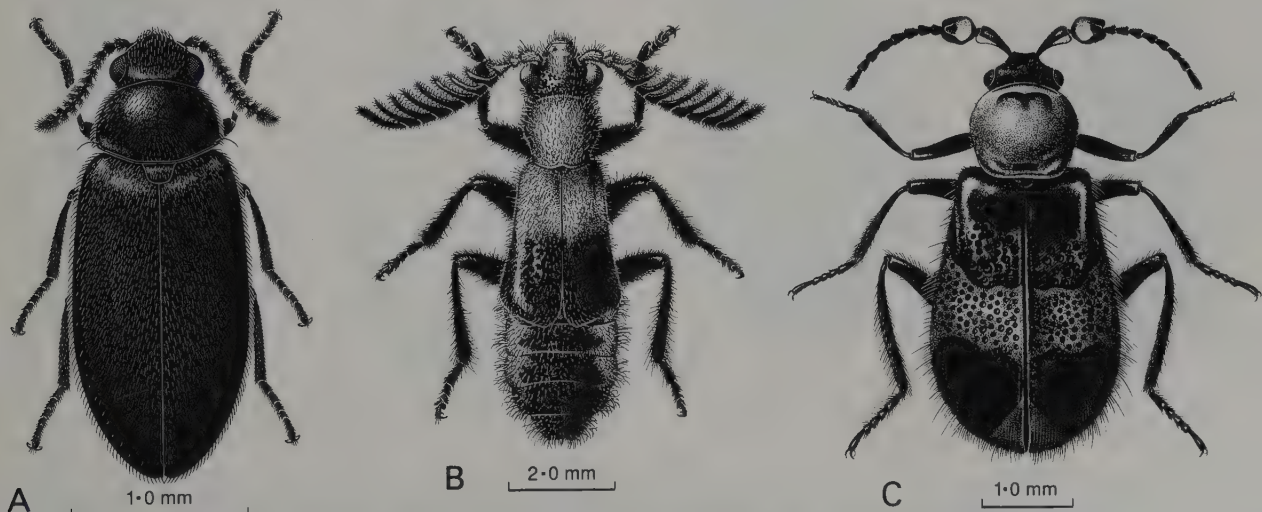


Fig. 35.45 Melyridae: A, *Dasytes bourgeoisi*, Dasytinae; B, *Balanophorus mastersi*, Malachiinae; C, *Dicranolaius bellulus*, Malachiinae.

[A by S. P. Kim; B by T. Nolan; C by F. Nanninga]



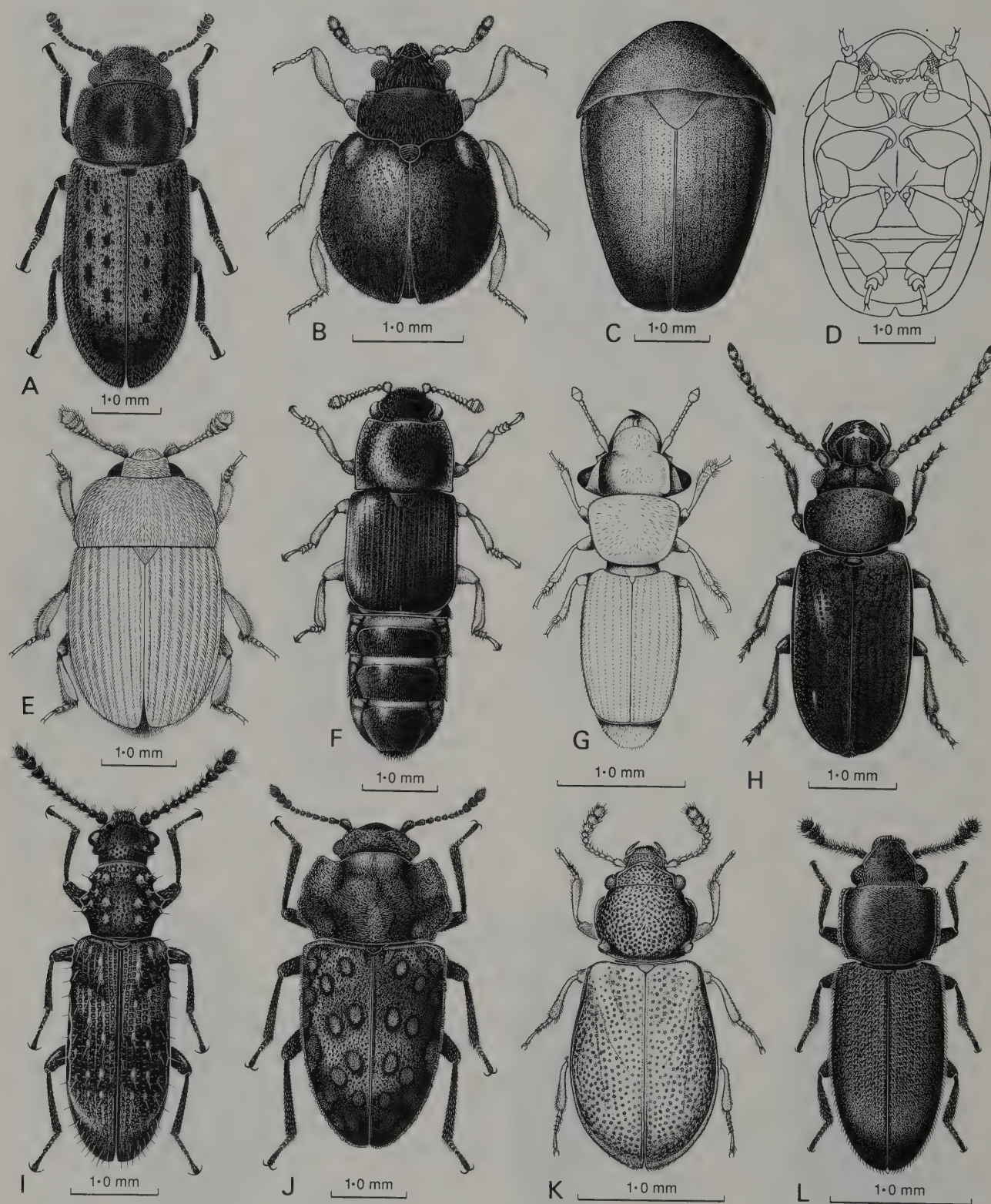


Fig. 35.46 Cucujoidea: A, *Ericmodes australis*, Protocucujidae; B, *Aspidiphorus humeralis*, Sphindidae; C–F, Nitidulidae: C, *Cychramptodes murrayi*, dorsal; D, same, ventral; E, *Idaethina pilistriata*; F, *Brachypeplus planus*; G, *Mimemodes laticeps*, Rhizophagidae; H, *Paracucujus rostratus*, Boganiidae; I–L, Phloeostichidae: I, *Hymaea magna*; J, *Priastichus tasmanicus*; K, *Tasmosalpingus* sp.; L, *Myrabolia grouvelliana*.

[A, I, J, L by S. P. Kim; B–D, H by A. Hastings; E, G by F. Nanninga; F by T. Nolan; K by S. Monteith]



related genera). In *Dicranolaius* and *Flabellolaius* the scape and 3rd (apparent 2nd) antennal segments are enlarged and distorted in the male. [Lea 1909; Wittmer 1952]

### Superfamily CUCUJOIDEA (Clavicornia)

Members of this group are usually distinguished from tenebrionoids by the presence of a cucujoid or ring-type aedeagus in the adult male and a more or less cylindrical, pygopod-like 10th abdominal segment in the larva. In adults, the trochanterofemoral attachment is rarely strongly oblique, females never have a 5-5-4 tarsal formula and there may be more than 4 veins behind MP; in larvae, the mandible usually has a prostheca, the mala is often falcate, and there may be 6 pairs of stemmata. Cucujoids are often difficult to distinguish from primitive members of the Cleroidea, and cleroid features (e.g. double tegmen, one tarsungular seta, no mandibular mola) occur in some cucujoid families. The present classification is somewhat tentative. The family Phloeostichidae may be further subdivided or variously combined with other members of the cucujid alliance, the positions of Lamingtoniidae and Helotidae are in doubt, and new family group taxa remain to be described (R. A. Crowson, T. Sen Gupta, S. A. Ślipiński unpubl.).

**61. Protocucujidae** (Fig. 35.46A). ADULT: ANT 11(3), FCOX TRANS(EXP), FCAV CLOS(OPEN), MCOX NARR-MWIDE(OPEN), 5-5-5/5-5-4♂, ABD 5(0), 3.8-5.5 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG +, SPIR AB.

Elongate, somewhat flattened beetles clothed with stout, decumbent setae. Head with strongly arched frontoclypeal suture resembling that in Sphindidae; antennal club weak; pronotum somewhat explanate laterally; tarsi densely setose below; elytra with deep window punctures and series of weak longitudinal elevations. Presumed larvae with tuberculate, mottled dorsal surface and distinctive T9 armed with ring of blunt processes in addition to urogomphi. This family, which also occurs in southern South America, includes several Australian species (one described) tentatively placed in *Ericmodes* but possibly including an undescribed genus. Tillyard (1926c) recorded *E. australis* from *Uromycladium* galls on *Acacia*, but specimens have also been taken in bark crevices, leaf litter and tree fern crowns, as well as in a river sample, where they probably originated in the forest canopy or on riparian vegetation. [Crowson 1955]

**62. Sphindidae** (Fig. 35.46B). ADULT: ANT 10(3), FCOX TRANS(EXP-CONC), FCAV OPEN(OPEN-CLOS), MCOX MWIDE(OPEN), 5-5-5/5-5-4♂, ABD 5(0), 1.3-2 mm. LARVA: HEAD PRO(PRO)/HYPO, STEM 6, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0/+, VER 0, LEGS 5, TS 2, UROG 0, SPIR AN.

Oblong to broadly ovate, convex beetles, usually finely pubescent with large, abrupt, tomentose antennal club. Frontoclypeal suture characteristically arched (Fig. 35.15E); mandibles with dorsal tubercle and setose cavity

like those in Boganiidae; elytral punctation seriate; tibial spurs usually absent; tarsi simple; pygidium usually slotted to receive elytral apices. Larvae elongate, tapered posteriorly and lightly sclerotised, except for head and weak tergal plates on either prothorax or abdominal segments 3-9; antennae usually more than half as long as head width. Both adult and larval Sphindidae feed on the spores of slime moulds (Myxomycetes). Most Australian species belong to *Aspidiphorus*, which is widely distributed in the Old World, but an undescribed genus occurs in Tas. and Vic. [Sen Gupta and Crowson 1979; Burakowski and Ślipiński 1987]

**63. Nitidulidae** (incl. Cybocephalidae; Figs 35.46C-F, 50A). ADULT: ANT 11(3), FCOX TRANS(EXP), FCAV OPEN-CLOS(CLOS), MCOX CONT-MWIDE (OPEN), 5-5-5/4-4-4R, ABD 5-6(0), 0.9-11 (1.5-5) mm. LARVA: HEAD PRO(PRO), STEM 2-4, ANT 3, FSUT 0/+R, LABR FR/FUR, MOLA +, VMP RET, MALA, MP 2-3, LP 1, HSC +, HRD 0/+R, VER 0, LEGS 5, TS 1R/2, UROG 0R/+, SPIR AB.

Usually oblong to ovate, less commonly elongate and parallel-sided, strongly convex to flattened beetles, usually brown or black, but occasionally bicoloured, and glabrous or pubescent. Antennal club almost always distinct; head usually abruptly constricted at base of clypeus; frontoclypeal suture almost always absent; labrum often emarginate or bilobed (sometimes concealed); maxilla almost always without galea and palp not expanded apically; hind coxae well separated; tibiae often expanded and serrate or spinose; first 4 tarsal segments often with expanded setose lobes; elytra complete or truncate, exposing one to several abdominal tergites. *Notobrachypterus* differs from other nitidulids in having a weak antennal club, a frontoclypeal suture and a distinct galea, while *Cybocephalus* is a minute, clambid-like form with only 4 tarsal segments. Larvae (Fig. 35.50A) oblong to elongate and subcylindrical to flattened, with dorsal surfaces often granulate or tuberculate and urogomphi (absent in *Cybocephalus* and *Notobrachypterus*) often accompanied by second pair of projections (pregomphi). Most nitidulids have the frontal arms widely separated at the base and the ventral mouth-parts deeply recessed, with longitudinally oblique cardines and blunt malae; however, frontal arms are contiguous in *Pocadius*, *Cybocephalus* and *Notobrachypterus* and cardines are only slightly oblique in the last genus. The mandibles are also distinctive in having a complex prostheca with fringes of comb-hairs (reduced in *Notobrachypterus* and absent in *Cybocephalus*). The spiracles of many nitidulid larvae are located at the ends of tubular processes.

Nitidulids have a wide variety of habits and habitats and those in Australia may be found in: leaf litter (*Stelidota*, *Thalycrodes*); rotten fruits (*Lasiodactylus*, *Carpophilus*); flowers of palms and *Pandanus* (*Platychoropsis*); dicotyledonous flowers (*Notobrachypterus*, *Aethina* (*Olliffura*)); seeds of Proteaceae and Sterculiaceae (*Idaethina*); rotten cactus (introduced *Camptodes*); mushrooms (*Cychramus*, *Pallodes*); puffballs (*Pocadius*); male cones of cycads (*Aethina* (*Circopes*)) or *Araucaria* (*Testudorea*); fermenting bark



or tree wounds (*Brachypeplus*, *Cryptarcha*, *Amphicrossus*); or preying on scale insects (*Cychramptodes*, *Cybocephalus*). Several introduced species, such as *Urophorus humeralis*, *Carpophilus hemipterus*, *C. davidsoni* and *C. dimidiatus* are pests of stored dried fruits, but may also attack ripe fruit in orchards. *Cychramptodes murrayi* (Figs 35.46C, D) may be seen feeding on the honeydew produced by the large females of *Cryptes baccatus* (HEMI: Coccoidea); they are protected from the tending ants by their ability to conceal all moving parts beneath the explanate and deflexed pronotum and elytral epipleura, and their larvae feed internally on the female and her brood. Kirejtshuk (1986b) divided the family into 7 subfamilies (KATERETINAE, CARPOPHILINAE, MELIGETHINAE, NITIDULINAE, CILLAEINAE, CRYPTARCHINAE and CYBOCEPHALINAE) [Hayashi 1978; Kirejtshuk 1986a, 1986c, 1987; Kirejtshuk and Lawrence 1990; Lawrence 1988a, 1991]

**64. Rhizophagidae** (Figs 35.46G, 50C). ADULT: ANT 10(1–2), FCOX GLOB(CONC), FCAV CLOS(CLOS), MCOX MWIDE(OPEN), 5-5-5/5-5-4♂/4-4-4, ABD 5(0), 1.4–5.3 mm. LARVA: HEAD PRO(PRO), STEM 0/2, ANT 3, FSUT 0, LABR FR/FU, MOLA +, VMP RET, MALA, MP 3, LP 1, HSC +, HRD 0/+, VER 0/+, LEGS 5, TS 2, UROG +, SPIR AB.

Elongate, parallel-sided, subcylindrical to flattened beetles, which may be glabrous or clothed with decumbent setae and have truncate elytra exposing pygidium. Except in *Shoguna*, head abruptly narrowed posteriorly, forming distinct *tempora* (temples) behind eyes, and pronotum crenulate or dentate laterally. Larvae (Fig. 35.50C) elongate, slightly flattened, slightly tapered posteriorly and lightly pigmented above but with tuberculate dorsal surface and sometimes lateral tergal processes on thorax and abdomen. Mala falciform; mandibular prosthema narrow and sometimes serrate; urogomphi weakly developed. Four genera occur in Australia, including the Asian *Monotomopsis*, which extends only into Cape York Peninsula. At least two introduced species of *Monotoma* occur in the more populated areas, where they are common inhabitants of grass piles or compost heaps. *Shoguna* species from North Qld are distinctive, subcylindrical, glabrous beetles, which have a long, narrow head and prothorax and may live in the tunnels of ambrosia beetles (Schedl 1962). Species of *Mimemodes*, which occur in Qld and northern N.S.W., may have a greatly expanded head in the male. Australian rhizophagids all appear to be mycophagous, feeding on moulds and other less conspicuous fungi. [Kuschel 1979]

**65. Boganiidae** (Fig. 35.46H). ADULT: ANT 11 (FIL/3), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX NARR–MWIDE(OPEN), P4-4-4, ABD 5(0), 1.7–4 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0, VER +, LEGS 5, TS 2, UROG +/0, SPIR AB.

Oblong, somewhat flattened, subglabrous or pubescent beetles with weak or no antennal club, distinct, straight frontoclypeal suture, membranous labrum concealed beneath clypeus, prominent mandibles bearing dorsal

tubercle and setose cavity, narrowly elongate maxillary palps and strongly transverse prothorax, which may have glandular callosities at anterior angles. In *Paracucujus* there is a distinct median endocarina extending posteriorly from the frontoclypeal suture and the clypeus is slightly elongate. Larvae elongate and tapered posteriorly, with sclerotised tergal plates on thorax and abdominal segments 1–9; urogomphi very short or absent; mala falcate and articulated; segment 10 with well-developed pair of adhesive pygopods. The family includes the Australian *Athertonium*, *Paracucujus* and *Boganium* and the South African *Metacucujus* and *Afroboganium*. *P. rostratus* occurs in south-western W.A., where adults and larvae feed on the pollen of *Macrozamia riedlei* (Cycadaceae). *Boganium* species occur in both dry and wet forests in eastern Australia and in mallee regions of western Vic., S.A. and W.A.; both larvae and adults are known to feed in *Eucalyptus* flowers. [Crowson 1990; Endrödy-Younga and Crowson 1986; Sen Gupta and Crowson 1966]

**66. Phloeostichidae** (Figs 35.46I–L, 50B). ADULT: ANT 11(3), FCOX TRANS–GLOB(EXP), FCAV OPEN (OPEN–CLOS), MCOX MWIDE(OPEN), 5-5-5/5-5-4♂, ABD 5(0/3), 1.6–6 mm. LARVA: HEAD PRO(PRO), STEM 5/6, ANT 3, FSUT 0, LABR FR/PF, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0/+, VER 0, LEGS 5, TS 2, UROG +, SPIR AN/AB.

This family is almost certainly a composite group which will be either subdivided or variously combined with other primitive cucujoid families. The four Australian genera each represent a distinct subfamily, two of which have representatives elsewhere; two more exotic subfamilies are based on the New Zealand *Agapytho* and the Palearctic *Phloeostichus*. HYMAEINAE (Fig. 35.46I) are usually narrowly elongate and fully winged, with shiny and tuberculate dorsal surfaces, dorsal mandibular tubercles and cavities, long and somewhat clavate femora, and apically expanded elytral sutural flange (except in the wingless *Hymaea succinifera*). In addition to *Hymaea*, this group includes an undescribed Australian genus and the Chilean *Rhopalobrachium*. Hymaeine larvae occur under bark and are elongate, parallel-sided and flattened, with widely separated urogomphi and curved rows of tergal and sternal asperities on the first 6 abdominal segments. PRIASILPHINAE includes the New Zealand *Priasilpha obscura* and the Tasmanian *Priastichus tasmanicus* (Fig. 35.46J). Adults are oblong, somewhat flattened and wingless, with a laterally explanate pronotum, widely separated coxae, and a dull and tuberculate upper surface bearing clusters of coarse, decumbent setae and often caked with debris. Larvae (Fig. 35.50B) are distinctive, flattened forms with complex lateral processes on thoracic and abdominal segments and with the abdominal spiracles located at the ends of these processes; both adults and larvae occur in leaf litter.

Species of *Myrabolia* (MYRABOLIINAE) (Fig. 35.46L) are elongate, flattened, pubescent, silvanid-like beetles, with a stridulatory file on the vertex, only slightly exposed fore trochantins, and a long first ventrite bearing a pair of setose cavities in the male. The genus is widely distributed in the southern part of the continent. Species



of *Tasmosalpingus* (TASMOSALPINGINAE) resemble small Salpingidae and were originally placed in that family. The most distinguishing feature of *Tasmosalpingus* (Fig. 35.46K) is the presence of a pair of setose cavities at the posterior angles of the pronotum and an additional pair just behind the elytral humeri; as in *Myrabolia* there is a stridulatory file on the vertex. The genus occurs in Vic. and Tas. [Crowson 1973a; Lawrence 1988a; Sen Gupta and Crowson 1966, 1969a]

**67. Silvanidae** (Figs 35.18L, Q, 47A, B). ADULT: ANT 8-9R/11(FIL/INCR/1R/2-4), FCOX GLOB(CONC), FCAV OPEN-CLOS(OPEN-CLOS), MCOX NARR-VWIDE (OPEN), 5-5-5/P4-4-4, ABD 5(2), 1.3-16 MM. LARVA: HEAD PRO(PRO), STEM 6, ANT 2/3, FSUT 0, LABR FR/PF, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG 0/+, SPIR AN.

Elongate, parallel-sided, more or less flattened, pubescent beetles with prognathous head, abruptly constricted posteriorly to form temples behind eyes, and pronotum often with projecting front angles and/or dentate or crenulate lateral margins. Fore coxal cavities visibly closed behind and tarsi with setose lobes below, except in the Uleiadini, which have a very long antennal scape (more than 5 times length of pedicel). Larvae (Figs 35.18L, Q) elongate, parallel-sided and lightly sclerotised, with broad head, long antennae and legs, reduced 9th abdominal segment, bearing a pair of slender urogomphi in most Uleiadini, and well-developed and terminal 10th segment. Silvanids are common in leaf litter and under bark, where they feed primarily on dead plant material and fungi. Several species, including *Ahasverus advena*, *Cryptamorpha desjardinsi*, *Monanus concinnulus*, *Nausibius clavicornis*, *Oryzaephilus mercator* and *O. surinamensis*, are cosmopolitan pests of stored foodstuffs. The Australian ULEIADINAE include *Dendrophagus australis* and several species of *Uleiota*, which occur under bark, a new genus (related to the New Zealand *Brontopriscus*) from North Qld, a few *Psammoeccus* mainly from Qld, and a large number of *Cryptamorpha* (many of them wingless), which are common litter inhabitants, especially in drier areas. The SILVANINAE include most of the introduced pests plus an endemic fauna including genera such as *Silvanus*, *Silvanolomus*, *Monanus* and *Austronausibius*. The genera *Nepharis* and *Nepharinus* include symphiles in the nests of *Iridomyrmex* and *Crematogaster*. [Crowson 1973a; Halstead 1973, 1980; Pal *et al.* 1984; Thomas 1984]

**68. Cucujidae** (incl. Passandridae; Figs 35.47C, D, 50D). ADULT: ANT 11(FIL/MON/INCR), FCOX GLOB(EXP-CONC), FCAV OPEN(OPEN), MCOX MOD-VWIDE(OPEN-CLOS), 5-5-5/5-5-4♂\*, ABD 5(3-4), 3.5-24 (7-20) MM. LARVA: HEAD PRO(PRO), STEM 0/6, ANT 2/3, FSUT 0, LABR FR/FU, MOLA 0/+, VMP RET/PRO, MALA, MP 2/3, LP 2, HSC 0/+, HRD 0/+, VER 0, LEGS 4R/5, TS 2, UROG 0/+, SPIR AN.

As here constituted, the Cucujidae includes the Passandrinae, which is often given family status, and excludes the Laemophloeidae and Silvanidae, which are sometimes considered as cucujid subfamilies. Adults are

elongate, parallel sided, cylindrical to strongly flattened, and glabrous, with large heads, relatively small eyes, antennae which are never distinctly clubbed, and a concealed labrum. In PASSANDRINAE, the body is more convex, the coxae relatively close together, the tibiae armed with apical teeth and sometimes enlarged spurs and the tarsi are simple; CUCUJINAE are much flatter, with widely separated coxae, unarmed tibiae and pubescent tarsi. *Platysus* is the only cucujine genus in Australia, and the larvae (Fig. 35.50D) are distinctive in being very flat and having a forked process at the apex of the abdomen; both adults and larvae occur under bark and are predacious. The Passandrinae are represented by *Passandra* (*Hectarthrum*), *Ancistria* and *Aulonostoma*; they live in the tunnels of wood-boring insects, where the 1st instars are active triungulins and later instars are ectoparasitoids. *Aulonostoma tenebrioides* often occurs in stored products, where it is parasitic on bostrichids, such as *Dinoderus* or *Lyctus*; it has been recorded from Papua New Guinea and probably occurs in Australia. [Aitken 1975; Gravely 1916; Ślipiński 1983, 1987a, 1989]

**69. Laemophloeidae** (Figs 35.18W, 47E). ADULT: ANT 11(FIL/MON/3), FCOX GLOB(CONC), FCAV OPEN/CLOS(OPEN), MCOX VWIDE(OPEN), 5-5-5/5-5-4, ABD 5(0), 1.5-3.5 MM. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP PRO, MALA, MP 3, LP 2, HSC 0, HRD +, VER 0, LEGS 5, TS 1, UROG +, SPIR AN/AU.

Elongate, parallel-sided and usually flattened, glabrous or pubescent beetles with a large, prognathous head, prominent mandibles, antennae which never have a very large or abrupt club and may have a modified scape in the male, a pronotum bearing a pair of longitudinal, submarginal carinae, and elytra which are often carinate. Larvae narrowly elongate, parallel sided, flattened and lightly sclerotised, except for head, 8th segment and T9. Head flattened, with moderately long antennae, paired dorsal endocarinae and long, parallel hypostomal rods; mandible with several hyaline processes near base of mesal edge; mala blunt; T9 forming articulated plate, and S9 and segment 10 reduced and concealed within emargination in S8 (Fig. 35.18W). The Australian fauna includes *Cryptolestes*, *Laemophloeus*, *Placonotus* and *Rhabdophloeus*. Laemophloeids usually feed on moulds or on the spores and stromata of various other Ascomycetes, but *Cryptolestes ferrugineus* and some related species are important pests of stored grains. [Lefkovitch 1959, 1962]

**70. Propalticidae** (Fig. 35.47F). ADULT: ANT 11(3), FCOX TRANS(CONC), FCAV OPEN(CLOS), MCOX VWIDE(CLOS), 5-5-5, ABD 5(0), 1.2-1.7 MM. LARVA (TENTATIVE): HEAD PRO(PRO), STEM 2, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP PRO, MALA, MP 3, LP 2, HSC 0, HRD +, VER 0, LEGS 5, TS 2, UROG 0, SPIR AN.

Minute, broadly ovate and strongly flattened beetles, clothed with short, decumbent, scale-like setae and with large head and eyes, a median endocarina on pronotum, strongly transverse scutellum, enlarged, serrate tibial spur on each fore leg, and very widely separated coxae. The



presumed larva is elongate, slightly flattened and lightly sclerotised, with very short antennae, several hyaline processes at the base of the mesal edge of the mandible,

paired parallel rods, as well as diverging hypostomal rods on the ventral side of the head, and a reduced and unsclerotised T9. Adults and larvae have been collected on or

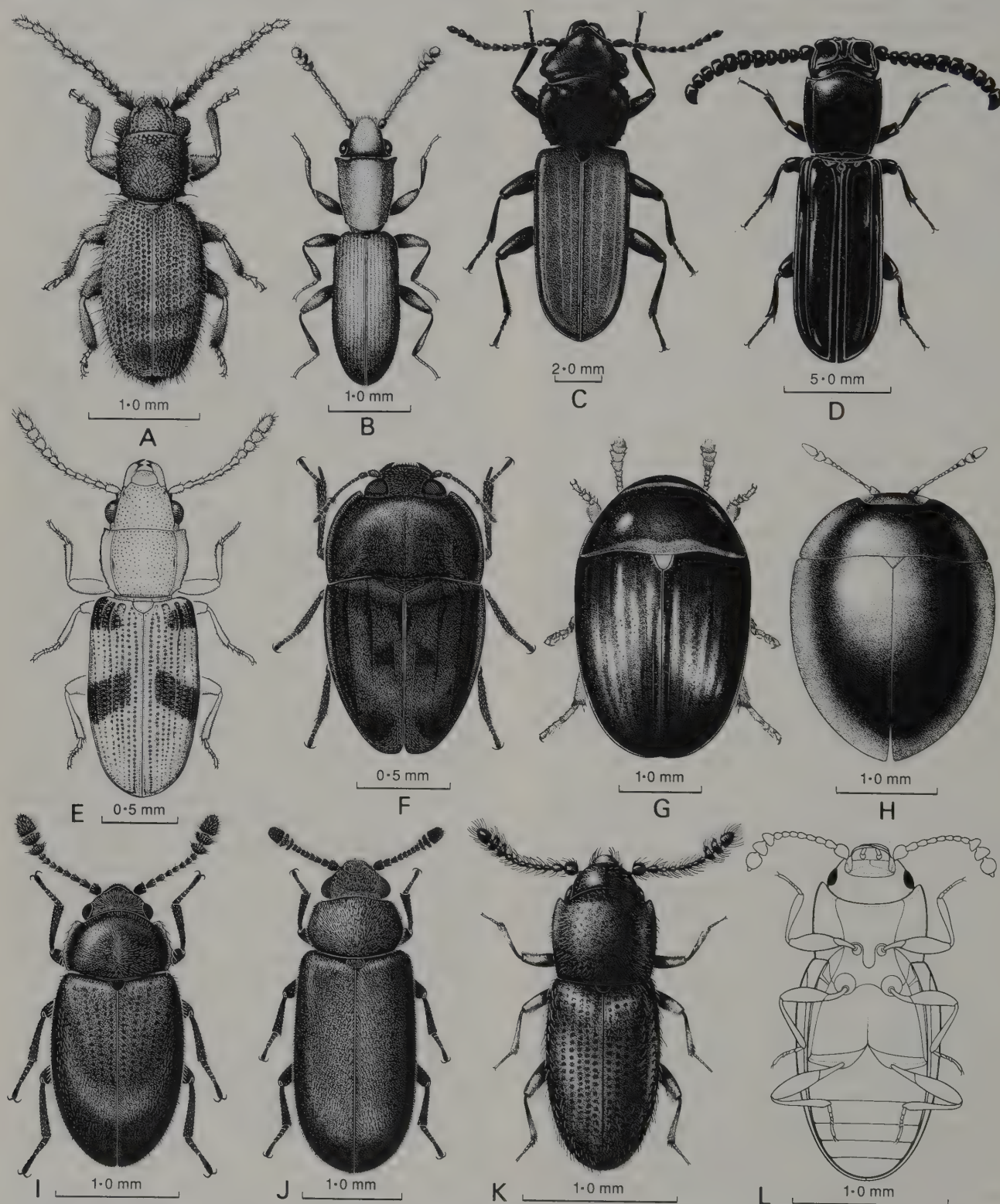


Fig. 35.47 Cucujoidea: A, *Cryptamorphia* sp., Silvanidae-Uleiottinae; B, *Silvanus unidentatus*, Silvanidae-Silvaninae; C, *Platys colonarius*, Cucujidae-Cucujinae; D, *Passandra heros*, Cucujidae-Passandrinae; E, *Laemophloeus amabilis*, Laemophloeidae; F, *Propalticus simplex*, Propalticidae; G, *Litochrus major*, Phalacridae; H, *Phalacrinus rotundus*, Phalacridae; I, *Hobartius* sp., Hobartiidae; J, *Cavognatha pullivora*, Cavognathidae; K, *Cryptophagus gibbipennis*, Cryptophagidae, dorsal; L, same, ventral.

[A by T. Nolan; B–D, H, K, L by F. Nanninga; E by S. Monteith; F, I, J by S. P. Kim; G by A. Hastings]



under the bark of standing trees or logs. The family is represented in Australia by several species of *Propalticus* from N.S.W. and Qld. The larva described as that of *P. simplex* by Crowson and Sen Gupta (1969) was misidentified. [John 1960]

**71. Phalacridae** (Figs 35.18v, 47g, ii). ADULT: ANT 11(3), FCOX GLOB-TRANS(CONC), FCAV OPEN (CLOS), MCOX NARR-VWIDE(CLOS), P4-4-4/4-4-4, ABD 5(0-2), 1-3.3 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 3, FSUT 0/+, LABR FR/PF/FU, MOLA 0/+, VMP PRO, MALA, MP 3, LP 2, HSC 0/+, HRD +, VER 0, LEGS 5, TS 1, UROG +, SPIR AN/AU/AB.

Broadly ovate, strongly convex, glabrous and shining beetles, in which lateral portions of prothorax and elytra are broadly explanate and deflexed. Head short, broad and deeply inserted into anterior prothoracic emargination; antennae relatively long with large club; tibiae with conspicuous setal comb at apex; tarsi with first 3 segments lobed and setose below and claws toothed or appendiculate. Larvae elongate and subcylindrical to flattened, usually narrowed posteriorly, and lightly sclerotised, except for head, protergal plate, apex of segment 8 and urogomphi or entire T9. Head broad and somewhat flattened, with short antennae and usually with median endocarina; mala blunt; hypostomal rods long and diverging; 8th spiracles located dorsally near posterior end of tergum; S9 and segment 10 more or less concealed (Fig. 35.18v). *Phalacrus* larvae are unusual in lacking an endocarina on the head and in having the antennal sensorium on segment 1, rather than 2. The major genera in Australia are *Phalacrinus*, *Phalacrus*, *Litochrus* and *Parasemus*. Phalacridae are primarily mycophagous and most feed on spores of various kinds; however larvae of *Litochrus* have been collected in rotten stringy bark and in rotten wood at the base of a living eucalypt. *Phalacrus uniformis* is known to feed on the spores produced on the galls of *Uromycladium* (Basidiomycetes: Uredinales), and *Phalacrinus* adults may be collected in numbers by beating dead eucalypt leaves. [Lea 1932; Steiner 1984; Thompson and Marshall 1980]

**72. Hobartiidae** (Fig. 35.47i). ADULT: ANT 11(3/5), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX MWIDE(OPEN), 5-5-5/5-5-4♂\*, ABD 5(0), 2.1-2.8 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 1, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG +, SPIR AB.

Oblong, convex, pubescent beetles with distinct antennal club (sometimes of leiodid type with reduced 2nd segment), well-developed, curved frontoclypeal suture, visible labrum, dorsal mandibular tubercles (but not cavities), finely crenulate or denticulate lateral pronotal carinae, and contiguous elytral apices (without expanded sutural flange). Larvae elongate, tapered posteriorly and relatively lightly sclerotised, with tuberculate dorsal surface, truncate or falcate mala, and 1-segmented labial palps. In addition to *Hobartius tasmanicus* and *Hydnobioides pubescens*, there are several other undescribed species in south-eastern Australia and in Argentina and Chile. Adults and larvae are known to feed in the softer

fruiting bodies of some Basidiomycetes, but adults may also be attracted to carrion-baited traps. [Sen Gupta and Crowson 1966, 1969a]

**73. Cavognathidae** (Fig. 35.47j). ADULT: ANT 11(3), FCOX TRANS(CONC), FCAV OPEN(OPEN), MCOX MWIDE(OPEN), 5-5-5, ABD 5(0), 2.2-3.1 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP RET, MALA, MP 3, LP 2, HSC 0, HRD +, VER 0, LEGS 5, TS 2, UROG +, SPIR AB.

Elongate, slightly flattened, pubescent beetles with apically widened sutural flanges on elytra, pair of cavities (usually joined by strongly curved impression) on frons, and simple prothorax with rounded angles and indistinct lateral carinae. Larvae elongate and parallel sided, with tergal plates on thoracic and most abdominal segments; mandibles with distinctive, forked hyaline process near base of mesal edge and no mola; mala falciform; with short, posteriorly projecting urogomphi. The family includes *Cavognatha* and *Taphropiestes*, both of which occur in Australia and South America, and *Neocercus* and *Zeonidicola*, which are restricted to New Zealand. Adults and larvae of *Cavognatha pullivora* and *Zeonidicola chathamensis* and adults of *Z. dumbletoni* and *Taphropiestes* sp. have been found in the nests of and sometimes on the nestlings of various bird species. [Crowson 1964a, 1973a; Sen Gupta and Crowson 1966, 1969a; Watt 1980]

**74. Cryptophagidae** (Figs 35.47k, l). ADULT: ANT 11(3), FCOX TRANS(CONC), FCAV OPEN (OPEN-CLOS), MCOX MWIDE-VWIDE(CLOS), 5-5-5/5-5-4♂\*, ABD 5(0), 1-2.8 mm. LARVA: HEAD PRO (PRO), STEM 0/1/2/5, ANT 3, FSUT 0, LABR FR/PF, MOLA +, VMP RET, MALA, MP 3, LP 1/2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG 0R/+, SPIR AN/AB.

Oblong to elongate and slightly flattened beetles, usually red or brown in colour and clothed with erect and decumbent hairs (rarely globose and/or glabrous). Antennal insertions exposed, lateral and well separated or more or less approximate; pronotum subquadrate with distinct lateral carinae or more rounded, sometimes with paired glandular callosities at anterior angles or near middle; prosternal process moderately broad and overlapping the mesosternum; elytra with apically widened sutural flanges and incomplete epipleura; trochanters more or less elongate; ventrite 1 much longer than 2. Larvae elongate, subcylindrical to flattened, and lightly sclerotised, with short and straight or sharply curved urogomphi (absent in one introduced species). Prostheca usually serrate and mala falcate. Cryptophagids feed on spores and hyphae of moulds and other fungi occurring under bark, in leaf litter or in nests of various kinds. Introduced species of *Cryptophagus*, *Henoticus*, *Atomaria*, *Anchicera* and *Ephistemus* may occur in foodstuffs and some are common in grass cuttings and compost heaps. The endemic Australian fauna, which is large and poorly studied, includes several genera with New Zealand and South American affinities. [Aitken 1975; Crowson 1980; M. E. G. Evans 1961b, 1961c]

**75. Lamingtoniidae** (Fig. 35.48a). ADULT: ANT 11(3), FCOX TRANS(EXP), FCAV OPEN(OPEN), MCOX



MWIDE(OPEN), 5-5-5, ABD 5(0), 2.8-3.4 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP PRO, MALA, MP 3, LP 2, HSC 0, HRD +, VER 0, LEGS 5, TS 2, UROG +, SPIR AB.

Oblong and slightly flattened, subglabrous beetles, yellowish to reddish brown with transverse dark band on elytra. Supra-antennal ridges sharply defined; distinct frontoclypeal prominence present; labrum not visible; mandible without mola but with setose, hyaline lobe and brush of hairs at base; ventrite 1 not much longer than 2. Larvae elongate and somewhat flattened, with paired endocarinae on head; long diverging hypostomal rods; acute, hyaline, mesal lobe at base of mandible; short urogomphi bearing accessory tubercles; and 8th spiracles located at the ends of long tubes. The single species, *Lamingtonium binnaburrense*, occurs in the rainforests of northern N.S.W. and southern Qld, where adults and larvae have been found feeding in a soft polypore fruiting body. [Sen Gupta and Crowson 1969b]

**76. Languriidae** (Figs 35.48B-D, 50t). ADULT: ANT 11(3-5), FCOX TRANS-GLOB(CONC), FCAV OPEN-CLOS(OPEN-CLOS), MCOX NARR-VWIDE(CLOS), 5-5-5, ABD 5(0), 1.5-10 mm. LARVA: HEAD PRO(PRO), STEM 0-2/5/6, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0/+, VER 0/+, LEGS 5, TS 2, UROG +, SPIR AN/AB.

Moderately to narrowly elongate, subcylindrical to slightly (occasionally strongly) flattened, setose to glabrous, and reddish brown in colour, sometimes with yellow markings or (Languriinae) with black or metallic blue elytra and red prothorax. Head large; eyes coarsely faceted; lateral pronotal margins almost always simple (rarely crenulate or with anterior callosities in *Leucohimatium*); tarsi with setose lobes beneath; elytral epipleura well developed and complete; ventrite 1 not much longer than 2. Larvae elongate, cylindrical to flattened, sometimes with lateral thoracic and abdominal processes (Fig. 35.50t), and moderately lightly sclerotised, sometimes with upper surfaces granulate or tuberculate. Urogomphi straight or curved, simple or complex; mandibular prosthema with broad base; mala falcate; head without median endocarina, except in *Leucohimatium*. The family, as here constituted, includes at least three distinct subgroups, some members of which have been placed in other families: XENOSCELINAE, LANGURIINAE and CRYPTOPHILINAE. A close relationship exists with Erotylidae and the two families are sometimes merged; the cryptophilines, on the other hand, have been combined with the exotic Toraminae in a separate family, Cryptophilidae (Crowson 1981). Among the Xenoscelinae, the widespread and introduced *Leucohimatium arundinaceum* has been found feeding on smut spores (Basidiomycetes: Uredinales) and occurs in stored products, *Loberus* has been found in decaying vegetation, and *Xenocryptus tenebroides* and some *Hapalips* have been found feeding on the pollen of cycads. *Cryptophilus* occurs in leaf litter and mouldy vegetation, and *C. integer* is a minor stored product pest with world-wide distribution. The Australian languriines are placed in the genera *Anadastus* and *Caenolanguria*; nothing is known of their

biology, but in some parts of the world languriine larvae are stem-borers. [Aitken 1975; Lawrence 1988a; Sen Gupta 1968a, 1968b; Sen Gupta and Crowson 1971]

**77. Erotylidae** (Figs 35.48E, 50g; Plate 5, B). ADULT: ANT 11(3/5), FCOX TRANS-GLOB(CONC), FCAV CLOS(OPEN), MCOX MWIDE-VWIDE(CLOS), 5-5-5, ABD 5(0), 3.2-25 (5-17) mm. LARVA: HEAD HYPO, STEM 5/6, ANT 3, FSUT 0, LABR FR, MOLA 0/+, VMP RET, MALA, MP 3, LP 2, HSC 0/+, HRD 0/+, VER 0/+, LEGS 5, TS 2, UROG 0R/+, SPIR AB.

Ovate to elongate, slightly flattened beetles, glabrous, except for *Cnecosa* and some *Thallis* species, and brightly patterned with red or yellow and black or occasionally metallic blue. Antennal club flattened in some larger species; apical palp segments often strongly expanded and securiform; lateral pronotal margins well developed, simple (or rarely undulate); prosternal process broad; femoral lines often on prosternum, metasternum or first ventrite; epipleura complete; tarsi lobed and setose beneath; ventrite 1 only slightly longer than 2. Larvae elongate and subcylindrical to slightly flattened, almost always with granulate upper surface and usually with last several tergites or at least T8 and T9 complexly tuberculate. Head more or less declined, sometimes with long median endocarina; large mandibles sometimes with basal mola replaced by setose, membranous lobe; mala truncate. The larva of *Microsternus* (Fig. 35.50g) is unusual in having a median spine on T9. Erotylidae are mycophagous and most of their larvae feed within the larger fruiting bodies of mushrooms and bracket fungi (Hymenomycetes: Agaricales and Aphyllophorales); adults often feed on the surfaces of fruiting bodies, but some may also feed internally. Most Australian erotylids belong to the DACNINAE and are placed in the genera *Thallis*, *Dacne* (introduced with dried mushrooms), *Episcaphula*, *Microsternus*, *Cnecosa* and *Hoplepiscapha*; there is some doubt, however, about the placement of the last 2 genera (Lawrence 1988a). In addition, *Hedista* (TRIPLACINAE) and *Encaustes* and *Micrencaustes* (ENCAUSTINAE) occur in North Qld. *Encaustes hercules* is the largest of our species. [Lea 1922b; Sen Gupta 1969]

**78. Biphyllidae** (Figs 35.48F, 50f). ADULT: ANT 11(2-3), FCOX TRANS(CONC), FCAV CLOS(CLOS), MCOX MWIDE(OPEN), 5-5-5/4-4-4, ABD 5(0), 1.4-8.5 mm. LARVA: HEAD PRO(PRO), STEM 6, ANT 3, FSUT 0, LABR PF, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD +, VER +, LEGS 5, TS 1, UROG 0/+R, SPIR AB.

Oblong to elongate, somewhat flattened, reddish brown to black or occasionally bicoloured beetles, densely clothed with erect and decumbent hairs. Eyes very coarsely faceted; pre-gular region with pair of setose cavities opening laterally just beneath eyes; pronotum with well-developed lateral margins, sometimes finely crenulate or serrulate, a pair of longitudinal, sublateral carinae, and occasionally an additional pair of basal grooves or foveae; femoral lines present on ventrite 1 and usually metasternum; penultimate tarsal segment reduced, preceding ones with membranous lobes beneath. Larvae (Fig. 35.50f) elongate, cylindrical and dorsally sclero-



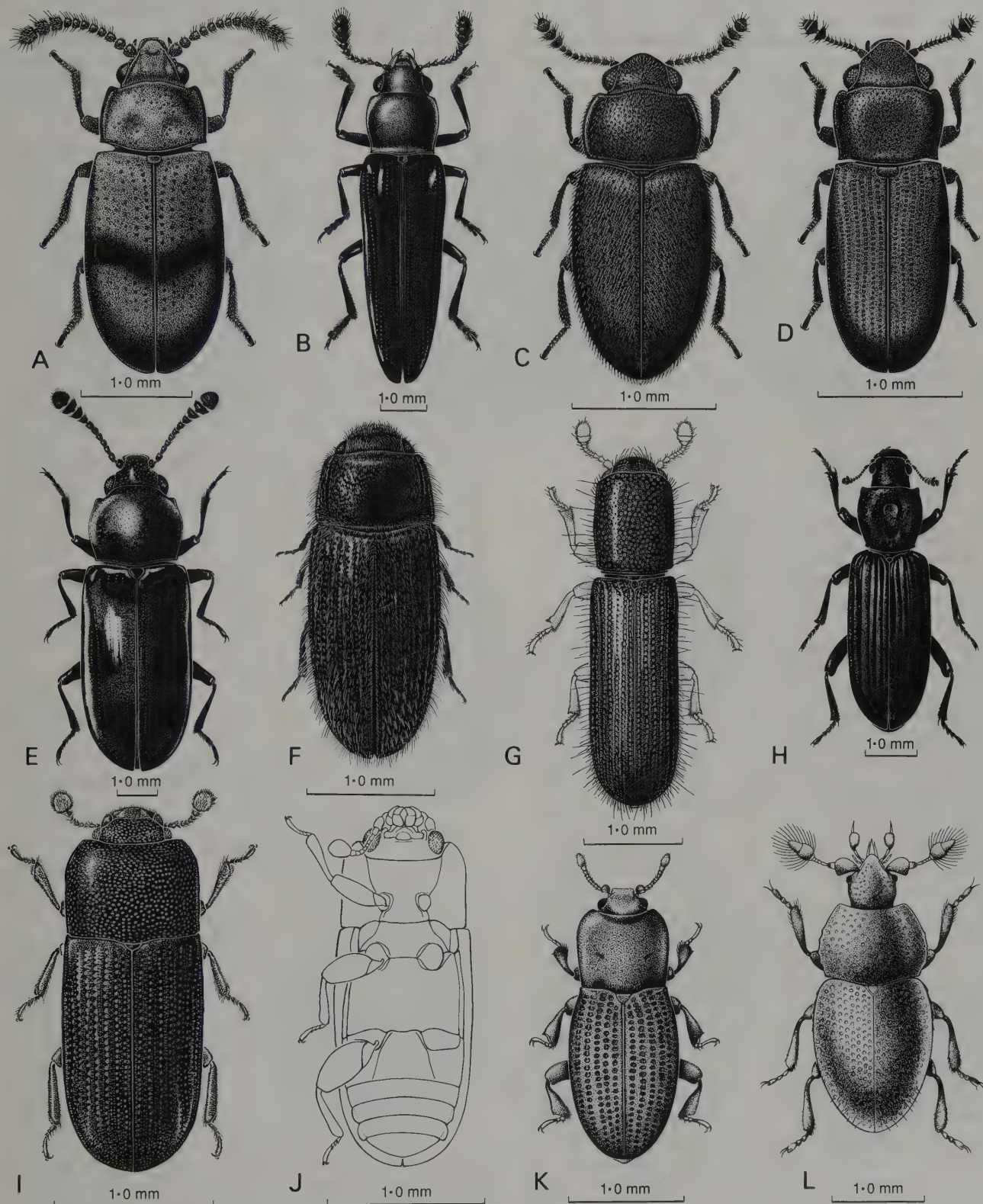


Fig. 35.48 Cucujoidea: A, *Lamingtonium binnaburrense*, Lamingtoniidae; B–D, Languriidae: B, *Caenolanguria vulgaris*, Languriinae; C, *Cryptophilus* sp., Cryptophilinae; D, *Xenoscelinus* sp., Cryptophilinae; E, *Thallis compta*, Erotylidae; F, *Diplocoelus punctatus*, Biphyllidae; G, H, Bothriderae: G, *Tereolaemus leae*, Tereolidae; H, *Ascetoderes aequinus*, Bothriderae; I–L, Cerylionidae: I, *Micruloma minuta*, Metacerylioninae, dorsal; J, same, ventral; K, *Cerylomopsis alienigenus*, Cerylioninae; L, *Cautomus mirabilis*, Cerylioninae. [A, C, D by S. P. Kim; B, E, F, H, K, L by F. Nanninga; G, I, J by S. Monteith]



tised, with complex mandibular prosthema bearing comb-hairs, falcate mala, and posterodorsally displaced 8th spiracles, usually borne on short tubes; T9 rarely with minute urogomphi; segment 10 terminal. Biphyllids may occur under bark or in leaf bases, especially when fermentation is occurring, but they also feed on and in the carbonaceous fruiting bodies of pyrenomycetous fungi, such as *Daldinia* and *Hypoxylon*. *Althaesia*, *Diplocoelus* and *Biphyllus* occur in Australia. [Lea 1922b; Nikitskii 1983]

**79. Bothrideridae** (Figs 35.48G, H, 50E). ADULT: ANT 10–11(1–3), FCOX GLOB–PROJ(CONC), FCAV OPEN–CLOS(OPEN), MCOX NARR–VWIDE(OPENR–CLOS), 4–4–4/3–3–3R, ABD 5(0), 1.5–13 MM. LARVA: HEAD PRO(PRO), STEM 0/6, ANT 2/3, FSUT 0, LABR FR/FU, MOLA 0/+, VMP RET, MALA, MP 2/3, LP 2, HSC 0/+, HRD 0/+, VER 0, LEGS 5, TS 0/1, UROG 0/+, SPIR AN/AB.

Oblong to narrowly elongate, subcylindrical to flattened beetles, usually subglabrous, but sometimes clothed with decumbent and erect hairs or rarely (*Dastarcus*) scale-like setae. Adults are superficially similar to some Colydiidae, from which they differ in having exposed antennal insertions and a cucujoid or ring-type aedeagus (p. 552). Antennae relatively short, usually with a compact, 1- or 2-segmented club (weakly 3-segmented in *Deretaphrus*); frontoclypeal suture usually present (sometimes indistinct); tibiae with expanded and spinose apices and sometimes enlarged and unequal tibial spurs; trochanterofemoral articulation strongly oblique, so that portion of femur is in contact with coxa (heteromeroid type), and in most species trochanter reduced and more or less concealed by femoral base. Larvae of *Xylariophilus*, *Anommatus* and the Teredinae are typically cucujoid with a granulate or tuberculate upper surface (Fig. 35.50E) and well-developed mandibular molae and urogomphi; those of Bothriderinae have no molae and minute or no urogomphi, and are either lightly sclerotised, physogastric ectoparasitoids or minute, fusiform triungulins. There are four subfamilies. The ANOMMATINAE includes the introduced *Anommatus duodecimstriatus*, which occurs in soil and leaf litter, and the XYLARIOPHILINAE is represented by *Xylariophilus* (2 spp.), which feed on the fruiting bodies of pyrenomycetous fungi in rainforests of Qld. The TEREDINAE are known to inhabit the tunnels of ambrosia beetles (Curculionidae: Platypodinae), but their larvae are not of the predacious type and probably feed on the yeasts cultivated by their hosts; there are several species of *Teredolaemus* in Australia. BOTHRIDERINAE feed on larvae and pupae of wood-boring insects, particularly Coleoptera (Buprestidae, Bostrichidae, Anobiidae, Cerambycidae, Curculionidae). These predacious or ectoparasitic forms construct silken cocoons or waxen chambers for pupation. Species of *Sosylus* appear to be restricted to the tunnels of ambrosia beetles and are known to have triungulin-like 1st instars and ectoparasitic late instars (Roberts 1980). Other bothriderine genera include *Deretaphrus* (the largest and most commonly encountered genus), *Dastarcus*, *Ascetoderes* and *Pseudobothrideres*. [Carter and Zeck 1937; Lawrence 1980, 1985b; Pal and Lawrence 1986]

**80. Cerylonidae** (Figs 35.48I–L, 50J). ADULT: ANT 8–11(1–3), FCOX GLOB(CONC), FCAV OPEN–CLOS(OPEN–CLOS), MCOX MWIDE–VWIDE(CLOS), 4–4–4/3–3–3, ABD 5(0), 0.8–3.1 MM. LARVA: HEAD PRO(PRO)/HYPO, STEM 0–2, ANT 3, FSUT 0, LABR FR/FU, MOLA 0/+, VMP RET, MALA, MP 3, LP 1/2, HSC 0/+, HRD 0/+, VER 0, LEGS 5, TS 1, UROG 0/+, SPIR AN/AB.

Broadly ovate to narrowly elongate, slightly to strongly flattened beetles, red to brown to black in colour (occasionally bicoloured) and subglabrous or sparsely clothed with erect hairs. Antennal club almost always 1- or 2-segmented and compact (3-segmented in *Protoxestus australicus*); hind coxae almost always widely separated; femoral lines often present on metasternum and/or ventrite 1. In Ceryloninae, maxillary palps aciculate, with reduced, narrow and acute apical segment and inflated penultimate one; frontoclypeal suture absent; mandibles and maxillae narrow and often styliform; and 5th ventrite with finely crenulate edge. In some cerylonines (e.g. *Cautomus mirabilis*, Fig. 35.48L) the labrum is acute and forms part of a sucking tube (Besuchet 1972). Larvae elongate to broadly ovate and disc-like (*Murmidius*, Fig. 35.50J) with lateral tergal processes on all thoracic and most abdominal segments and usually with granulate or tuberculate dorsal surface clothed with variously modified setae. The mouth-parts may be mandibulate, but in Ceryloninae they are styliform and either endognathous or enclosed within a sucking tube (Fig. 35.16G). The Australian species belong to four subfamilies: EUXESTINAE (*Protoxestus*, *Euxestus* and *Hypodacnella*), METACERYLONINAE (*Micruloma*), MURMIDIINAE (the introduced *Murmidius ovalis*), and CERYLONINAE (*Australiorylon*, *Cautomus*, *Cerylonopsis*, *Lawrencella*, *Mychocerus*, *Philothermus*). Cerylonids are commonly found under bark of rotten logs and in decaying leaf litter, where they probably feed on fungal hyphae and spores, and possibly slime mould plasmodium. *M. ovalis* occurs in stored food which has been contaminated with moulds or yeasts; it is not considered to be a pest. [Halstead 1968; Pal and Lawrence 1986; Sen Gupta and Crowson 1973; Ślipiński 1988]

**81. Discolomidae** (Fig. 35.49E). ADULT: ANT 9(1), FCOX GLOB(CONC), FCAV CLOS(OPEN), MCOX VWIDE(CLOS), 3–3–3, 5(0), 1.3–2 MM. LARVA: HEAD PRO(PRO), STEM 3, ANT 2, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 2, LP 2, HSC 0, HRD 0, VER 0, LEGS 5, TS 1, UROG 0, SPIR AN.

Broadly ovate and flattened, subglabrous or pubescent beetles with more or less explanate side margins bearing glandular pores on both prothorax and elytra. Antennae distinctive, having enlarged and expanded terminal segment forming club; frontoclypeal suture present; ventrite 1 much longer than 2; all coxae small and globose with long internal extensions. Larvae broadly ovate, flattened and disc-like, with head more or less concealed from above and vestiture consisting of club-like setae around edges and star-shaped scales on dorsal surface. Discolomids may be collected in leaf litter or under bark, and they are known to feed on the fruiting bodies of vari-



ous polypore fungi. The Australian species all belong to the genus *Aphanocephalus*. [Fukuda 1969; John 1959; Lea 1922b]

**82. Endomychidae** (incl. Merophysiidae; Figs 35.49A, 50H; Plate 5, G). ADULT: ANT 4R, 8–11(1–3), FCOX LOB(CONC), OPEN–CLOS<sub>R</sub>(CLOS), MCOX MWIDE–VWIDE(OPEN–CLOS), 4-4-4/P3-3-3/3-3-3, ABD 5/

6(0), 1–7.5 mm. LARVA: HEAD PRO(PRO) /HYPO, STEM 0–4, ANT 3, FSUT 0/+, LABR FR, MOLA 0/+, VMP RET, MALA, MP 3, LP 2, HSC 0/+, HRD 0/+, VER 0, LEGS 5, TS 1, UROG 0/+<sub>R</sub>, SPIR AN/AU/AB.

Broadly ovate to elongate and globose to moderately flattened beetles, glabrous or clothed with decumbent and erect hairs, often brightly patterned with red or yellow

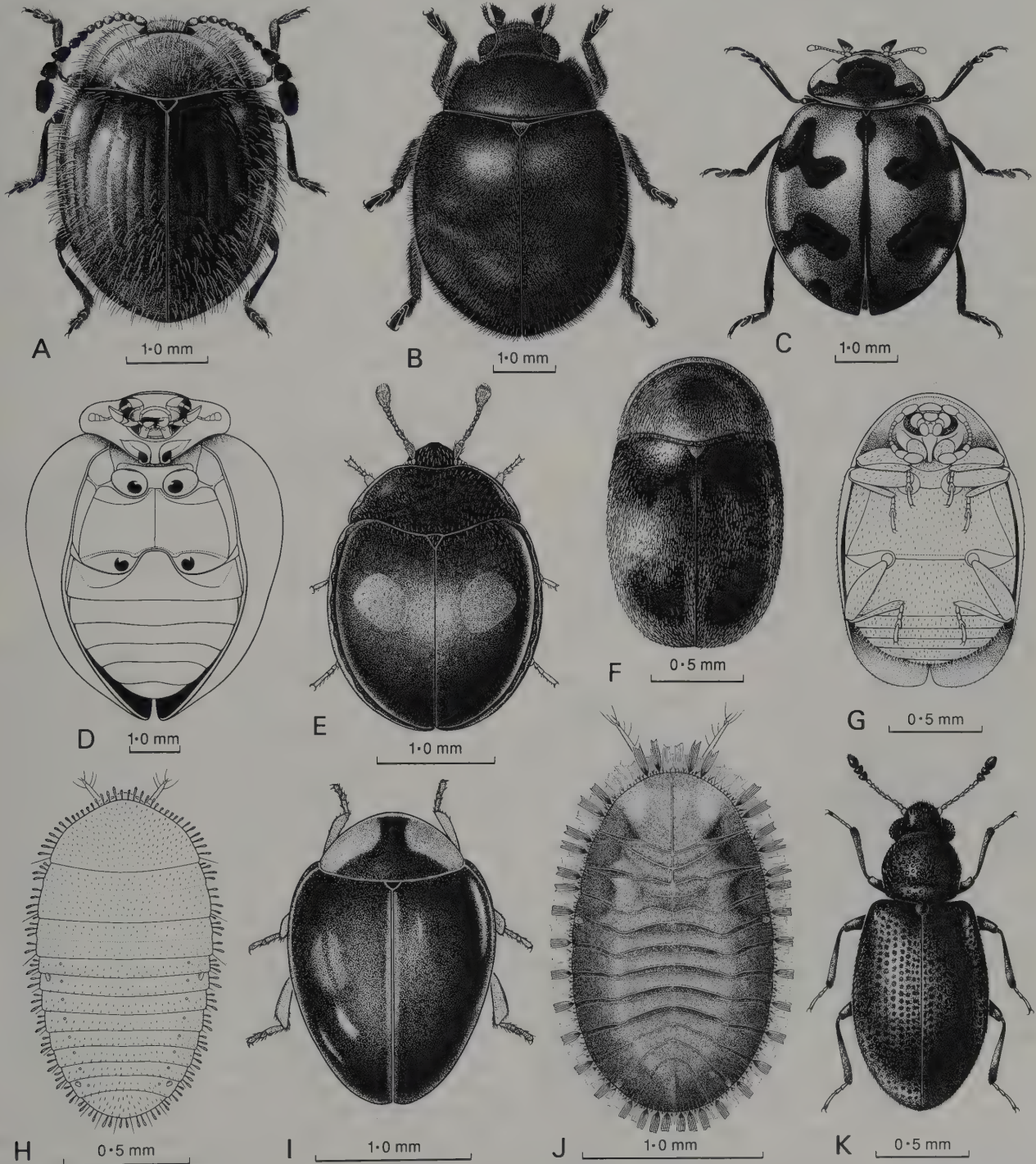


Fig. 35.49 Cucujoidea: A, *Stenotarsus pisoniae*, Endomychidae; B–D, Coccinellidae: B, *Scymnodes bellus*, Scymninae; C, *Coccinella transversalis*, Coccinellinae; D, *Epilachna guttatopustulata*, Epilachninae; E, *Aphanocephalus bimaculatus*, Discolomidae; F–J, Corylophidae: F, *?Alloparmulus pulchellus*, Saciinae, dorsal; G, same, ventral; H, *Corylophodes* sp., Corylophinae, larva; I, same, adult; J, *?Lewisium* sp., Corylophinae, larva, dorsal; K, *Corticara hirtalis*, Lathridiidae-Corticariinae.

[A, C, D, F, G, K by F. Nanninga; B after Pope and Lawrence 1990, reprinted with permission of Blackwell Scientific Publications; H, J by S. P. Kim; E, I by A. Hastings]



and black. Frontoclypeal suture present; antennae moderately long, usually with relatively loose club; maxillary palps fusiform, although labial palps may be securiform; 2nd tarsal segment commonly lobed, extending beneath reduced 3rd segment; tarsal claws simple; femoral lines on first ventrite lacking (except in a few exotic species). Larvae (Fig. 35.50H) usually oblong to ovate (rarely elongate), slightly to strongly flattened, usually with lateral tergal processes on all thoracic and most abdominal segments and only rarely with short urogomphi. In *Encymon immaculatus* these processes are spinose and deciduous, breaking off when grasped by a predator. Antennae often long (with segment 2 elongate and 1 and 3 reduced), their sockets well separated from the mandibular articulations; head often broad at base and strongly narrowed towards the mouth-parts; mala obtuse. Endomychids feed on a wide variety of fungi, but little is known about the feeding habits of most Australian species. The widely distributed *Trochoideus desjardinsi*, known to inhabit termite fungus gardens in Java (Kemner 1924), is a general fungus feeder on Christmas and Cocos-Keeling Is. *Mycetaea subterranea* and *Holoparamesus depressus* are introduced contaminants of mouldy food stores. The largest number of species occur in *Stenotarsus* and *Periptectus*; the latter is a peculiar endemic group occurring in leaf litter in wet montane habitats. [Sasaji 1978; Lea 1922b; Strohecker 1953]

**83. Coccinellidae** (ladybird beetles; Figs 35.49B–D, 50K). ADULT: ANT 7–11(INCR/1–6), FCOX TRANS(CONC), FCAV OPEN(CLOS), MCOX MWIDE–VWIDE(OPEN), 3-3-3R/P3-3-3, ABD 5/6(2), 0.9–11 MM. LARVA: HEAD PRO(PRO/HYPO), STEM 3, ANT 1–3, FSUT 0/+, LABR FR, MOLA 0/PSR, VMP RET, MALA, MP 2/3, LP 1/2, HSC 0/+R, HRD 0/+, VER 0, LEGS 5, TS 1, UROG 0, SPIR AN.

Broadly ovate, moderately to strongly convex beetles with pseudotrimerous tarsi (segment 3 reduced, 2 strongly lobed beneath it). Antennae short, weakly clubbed; apical maxillary palp segment almost always large and securiform; femoral lines on first ventrite and sometimes metasternum. Many larger species glabrous and brightly patterned with red or yellow and black or blue; most smaller species more uniformly coloured and finely pubescent. Larvae (Fig. 35.50K) elongate, oblong or occasionally broadly ovate and slightly to strongly flattened, usually with transverse row of 6 tubercles or prominences on most abdominal segments and often covered with waxy exudate; some forms are spinose above and may be aposematically coloured (pp. 99, 561) like many adults. Antennae very short; mandibles often with sub-basal lobe which probably represents a reduced mola; mala obtuse and usually with *stylus* (specialised, setiferous process); there are paired glandular openings on the thorax and abdomen; tibia usually with 2 to several expanded setae extending beneath tarsungulus. Pupa obtect and partly enclosed within larval skin, which is attached to substrate by anal end.

Adults and larvae of most species are predacious on aphids, mealybugs, scales or other small insects and mites. The Epilachninae, however, are phytophagous,

*Epilachna* damaging the foliage of Solanaceae and Cucurbitaceae, including vegetable crops like pumpkin, cucumber, tomato and potato; while the Psyllorborini (Coccinellinae) feed on powdery mildews (Ascomycetes: Erysiphales). Among the carnivorous species, several have been used with notable success as agents of biological control. *Rodolia cardinalis*, for instance, saved the California citrus industry from destruction by the cottony cushion scale (*Icerya purchasi*), while other Australian species, such as *Cryptolaemus montrouzieri*, *Rhyzobius ventralis* and *R. forestieri*, were employed in Hawaii and California for the control of a number of scale insects (HEMI: Coccoidea). Species of *Stethorus* are predators of the two-spotted mite (*Tetranychus urticae*) (Britton and Lee 1972). Some adult coccinellids, when alarmed, feign death and discharge drops of yellow haemolymph, which is toxic to vertebrates, from the tibio-femoral articulations. There are 6 subfamilies: STICHOLOTIDINAE, SCYMNINAE, CHILOCORINAE, COCCIDULINAE, COCCINELLINAE and EPILOCHNINAE. Among the larger and more commonly encountered Australian coccinellines are *Coelophora inaequalis*, *Coccinella transversalis* and *Harmonia conformis*. [Gordon 1985; Hagen 1962; Hodek 1973; Pope 1979, 1981, 1989; A. M. Richards 1981, 1983; Sasaji 1968, 1971]

**84. Corylophidae** (Figs 35.49F–J). ADULT: ANT 8–11(3/5), FCOX TRANS–GLOB(CONC), FCAV OPEN–CLOS(CLOS), MCOX MWIDE–VWIDE(OPEN–CLOS), 4-4-4/P3-3-3, ABD 5/6(0), 0.6–2 MM. LARVA: HEAD PRO(PRO), STEM 1/2, ANT 2/3, FSUT 0, LABR FR/FU, MOLA 0/+, VMP RET/PRO, MALA, MP 2/3, LP 1/2, HSC 0/+, HRD 0/+, VER 0, LEGS 5, TS 1, UROG 0, SPIR AN.

Minute, oblong to broadly ovate and strongly convex to somewhat flattened beetles (rarely more elongate and flattened), with small head usually concealed beneath prothorax and relatively long antennae with large club. *Orthoperus*, *Corylophodini* and *Rypobiini* (Corylophinae) are glabrous, while *Priamima*, *Sericoderinae* and *Saciinae* are almost always pubescent. The elytra are truncate, exposing the abdominal apex, in *Orthoperini*, *Saciinae* and *Sericoderinae*, and in the last group the hind angles of the pronotum extend posteriorly to embrace the elytral humeri. In *Rypobiini*, the labrum is acute and the mandibles and maxillae are stylet-like (Pakaluk 1987). Larvae oblong to broadly ovate (Figs 35.49H, J), more or less flattened and clothed with variously modified setae, with paired glandular openings on abdominal segments 1 to 7 or 1 and 8. Antennae moderately to very long; head transverse to somewhat elongate; mouth-parts sometimes stylet-like and endognathous; tarsungular seta usually clavate. *Sericoderus* and *Orthoperus* occur commonly in grass cuttings and mouldy hay, and *Corylophodes* and *Rypobiini* have been taken in leaf litter samples. Some *Saciinae* and *Sericoderinae* have been collected feeding on surface spore fields produced by certain Ascomycetes. Corylophids have also been collected under bark, in rotten wood and on the pore surfaces of bracket fungi. As in Coccinellidae, the pupa is obtect and partly enclosed within the larval skin. There are 3 subfamilies in



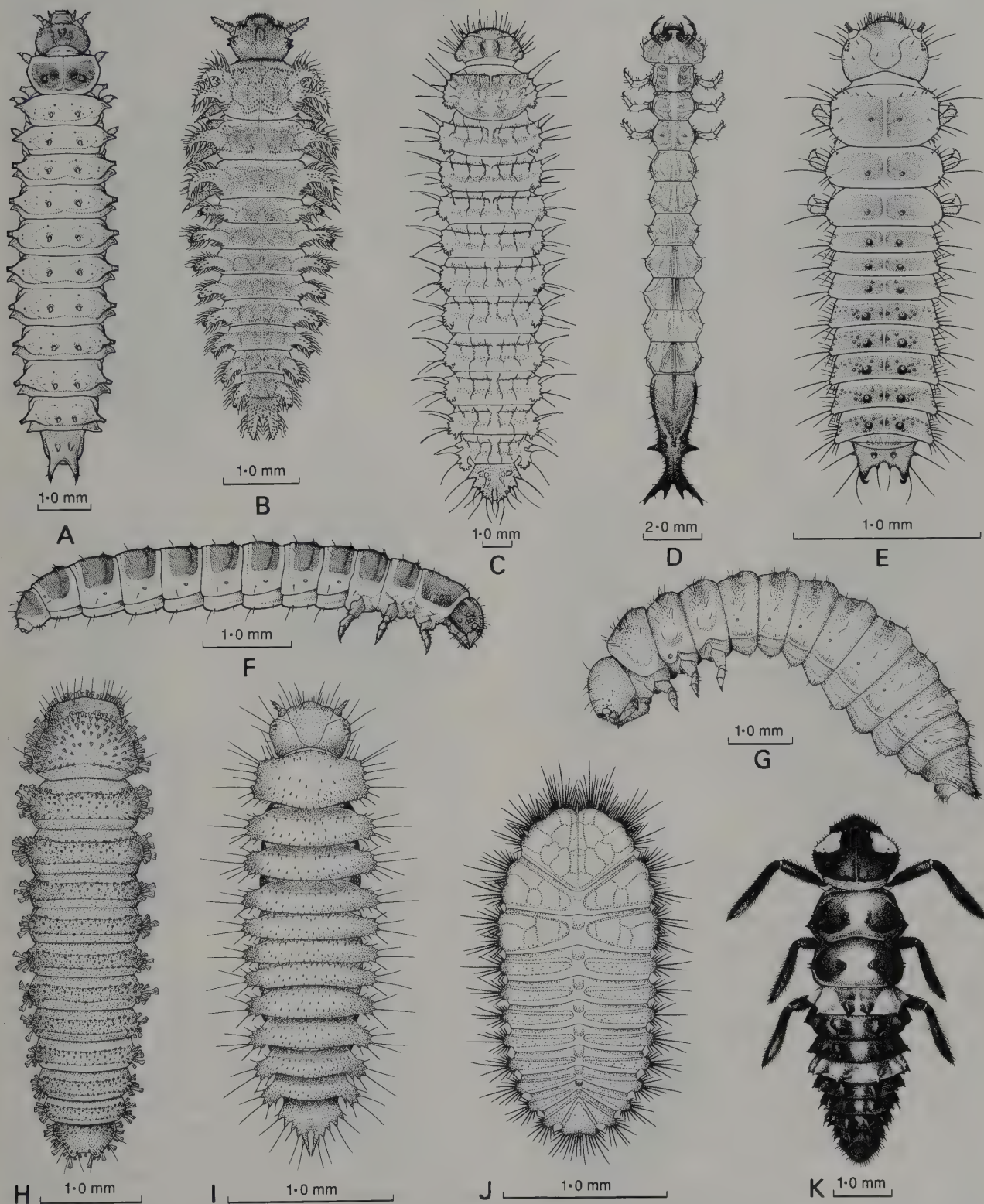


Fig. 35.50 Larvae of Cucujoidea: A, *Lasiodactylus* sp., Nitidulidae; B, *Priastichus tasmanicus*, Phloeostichidae-Priasilphinae; C, *Monotoma americana*, Rhizophagidae; D, *Platisus moerosus*, Cucujidae-Cucujinae; E, *Teredolaemus leae*, Bothrididae-Teredinae; F, *Diplocoelus fasciatus*, Biphyllidae; G, *Microsternus* sp., Erotylidae-Dacninae; H, *Mycetaea subterranea*, Endomychidae; I, *Cryptophilus* sp., Languriidae-Cryptophiliinae; J, *Murmidius ovalis*, Cerylonidae-Murmidiinae; K, *Coccinella transversalis*, Coccinellidae-Coccinellinae.

[A, F by T. Nolan; B by S. Smith; C by S. Poulakis; D, K by F. Nanninga; E, G-J by S. P. Kim]



Australia: SERICODERINAE (*Anisomeristes*, *Sericoderus*), SACHIINAE and CORYLOPHINAE (*Orthoperus*, *Priammina*, *Corylophini*, *Corylophodini*, *Rypobiini*). [Pakaluk and Lawrence 1986; Paulian 1950, 1962]

**85. Lathridiidae** (Fig. 35.49k). ADULT: ANT 10–11(2–3), FCOX PROJ(CONC), FCAV CLOS(CLOS), MCOX CONT-MWIDE(CLOS), 3-3-3, ABD 5–6(0), 0.8–2 mm. LARVA: HEAD PRO(PRO), STEM 1–5, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET/PRO, MALA, MP 3, LP 1/2, HSC +, HRD 0/+, VER 0, LEGS 5, TS 1, UROG 0, SPIR AN.

Minute beetles with pronotum usually much narrower than elytral bases, elytral punctures more or less seriate, clypeus laterally expanded in front of antennal insertions, and antennal scape usually large and more or less globular. LATHRIDIIDAE subglabrous with median groove on frons, separated fore coxae, and usually carinae on pronotum or elytra and waxy exudate covering various portions of body; CORTICARIINAE usually setose with contiguous fore coxae and no carinae or waxy exudate. Larvae elongate, tapered posteriorly, and lightly sclerotised except for head, with vestiture of long, fine setae or occasionally shorter, frayed setae. Antennae relatively long; mandibles often partly membranous; mala obtuse. Adults and larvae feed on the spores of a variety of fungi and are commonly taken from dead vegetation and leaf litter. Some *Enicmus* are found in the fruiting bodies of slime moulds (*Myxomycetes*), while other lathridiids specialise on moulds or other ascomycetous fungi. *Corticaria hirtalis* is often beaten from foliage. Several Australian species, such as *Lathridius minutus*, *Cartodere constricta*, *Dienerella* spp., *Adistemia watsoni*, *Corticaria japonica*, *C. elongata* and *C. ferruginea*, have been introduced in ballast or mouldy food stores, while others, like *Aridius nodifer*, *A. bifasciatus* and *A. australicus*, are probably endemic taxa which have been widely introduced to other parts of the world. [Aitken 1975; Hinton 1945a; C. Johnson 1975; Watt 1969]

### Superfamily TENEBRIONOIDEA (Heteromera)

Basic features of adult tenebrionoids include 5-5-4 tarsi in both sexes (with reduction to 4-4-4 in several lineages), strongly oblique or heteromeroid trochanterofemoral attachment, reduction in the number of wing veins behind MP to 4 or fewer, heteromeroid type of aedeagus, in which the incomplete tegmen lies above the penis (orientation reversed in some groups), and a tendency for the fore coxae to be conical and projecting or partly concealed by the pronotal cowl and their trochantins to be reduced and/or concealed. Larvae have fewer than 6 stemmata on each side, a blunt mala, no mandibular protheca, and a 10th segment which is transverse or somewhat rectangular but not forming a cylindrical pygopod.

The present classification is far from satisfactory; preliminary discussions of family relationships were given by Crowson (1955, 1966b, 1967), Lawrence (1977) and Lawrence and Newton (1982), and contributions to the classification of particular lineages, often based in part on newly discovered larval types, have been made by

Crowson and Viedma (1964), Doyen and Lawrence (1979), Doyen and Tschinkel (1982), Hayashi (1969, 1975), Lawrence (1974, 1977, 1980, 1987b), Watt (1967, 1974a, 1974b, 1987) and D. K. Young (1976, 1978, 1985a, 1985b). The arrangement used here follows Lawrence (1982) for the most part and differs from that in Britton (1970) as follows: transfer of the colydiid subfamily Bothriderinae to the Cucujoidea (as a family); transfer of the cucujid genus *Prostomis* to the Tenebrionoidea (as the family Prostomidae); inclusion of Merycidae in Zopheridae, Lagriidae and Alleculidae in Tenebrionidae, Inopeplidae, Elacatidae and *Tenebrionidae* (from Tenebrionidae) in Salpingidae, Hemipeplidae in Mycteridae, and *Lagrioida* (from Oedemeridae) in Anthicidae.

**86. Mycetophagidae** (Fig. 35.51b). ADULT: ANT 11(3–4), FCOX TRANS(EXP-CONC), FCAV OPEN(CLOS), MCOX CONT-NARR(OPEN), 4-4-4/3-4-4 3\*, ABD 5(0), 1.5–3.6 mm. LARVA: HEAD PRO(PRO), STEM 4/5, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG +, SPIR AN/AU/AB.

Oblong to ovate, somewhat flattened beetles, uniformly brown or with yellow maculae on elytra, and densely pubescent. Eyes relatively large and coarsely faceted; frontoclypeal suture present or absent; tibial spurs often well developed and serrate; fore tarsi modified in male. Larvae elongate and parallel sided, slightly flattened and moderately sclerotised dorsally, with well-developed legs and slightly curved, simple urogomphi, which are more or less approximate at base. Adults and larvae are primarily mycophagous and may be found in rotten wood or associated with fungus fruiting bodies. Several endemic *Litargus* are known from Australia, and three introduced species, *Litargus balteatus*, *Mycetophagus quadriguttatus* and *Typhaea stercora*, occur in stored foodstuffs affected by mould. [Aitken 1975; Hinton 1945a; Lawrence 1987b]

**87. Archeocrypticidae** (Fig. 35.51a). ADULT: ANT 11(2/3/5/7), FCOX GLOB(CONC), FCAV CLOS(CLOS), MCOX MWIDE(OPEN), 5-5-4, ABD 5(2), 1.5–3.7 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT +, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG 2, SPIR AB.

More or less ovate, slightly flattened, finely pubescent, black or brown beetles. Frontoclypeal suture distinct; apical segment of maxillary palp expanded and truncate; lateral pronotal margins well developed; prosternal process abruptly expanded apically; tibiae more or less spinose. Larvae elongate, parallel sided, slightly flattened and lightly sclerotised, with simple, acute, posteriorly projecting urogomphi which are well separated at base. Adult and larval archeocrypticids may be found in leaf litter or in the softer fruiting bodies of some polypores, such as *Piptoporus*. There are several Australian genera, including *Enneboeus*, *Enneboeopsis*, *Wattianus*, *Sivacrypticus* and *Archeocrypticus*. [Kasab 1984]

**88. Ciidae** (Fig. 35.51e). ADULT: ANT 8–10(2–3), FCOX TRANS-PROJ(CONC), FCAV OPEN(OPEN), MCOX CONT(OPEN), 4-4-4, ABD 5(0), 1.1–3.3 mm.



LARVA: HEAD HYPO, STEM 0-5, ANT 2, FSUT 0, LABR FR, MOLA 0/PSR, VMP RET, GLAC/MALA, MP 3, LP 2, HSC 0, HRD 0, VER +, LEGS 5, TS 2, UROG 0/+, SPIR AN.

Elongate and subcylindrical or moderately flattened to ovate and globose beetles, subglabrous or clothed with decumbent and/or erect hairs or bristles. Head more or less deflexed, usually with distinct frontoclypeal ridge

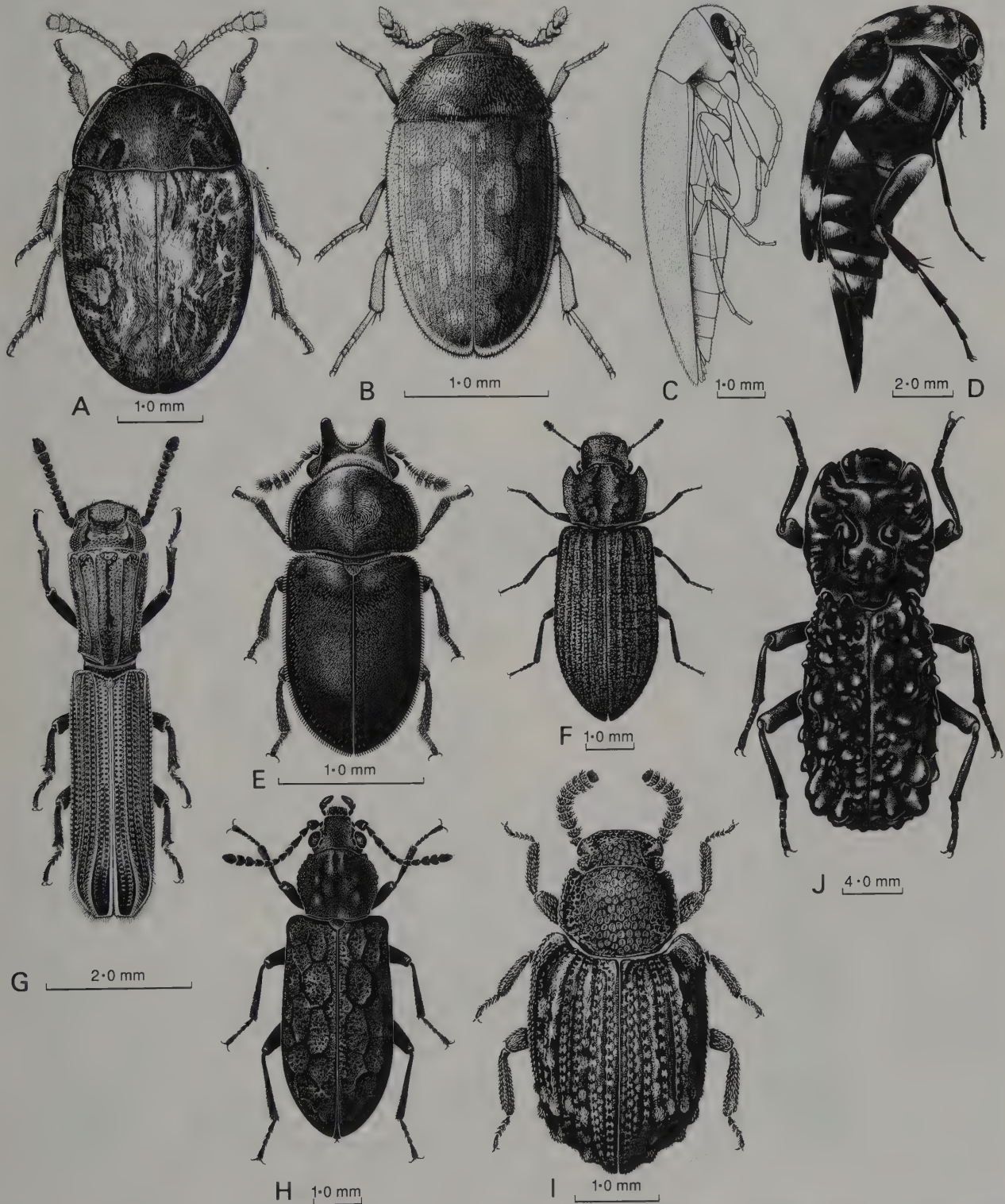


Fig. 35.51 Tenebrionoidea: A, *Wattianus queenslandicus*, Archeocrypticidae; B, *Litargus multiguttatus*, Mycetophagidae; C, *Talayra elongata*, Melandryidae; D, *Hoshihananomia leucosticta*, Mordellidae; E, *Cis cervus*, Ciidae; F, G, Colydiidae: F, *Sparactus elongatus*; G, *Pseudendestes australis*; H-J, Zopheridae: H, *Meryx rugosa*; I, *Cotulades* sp.; J, *Zopherosis georgei*.

[A by A. Hastings; B by T. Nolan; C, D, F, H, J by F. Nanninga; E by S. P. Kim; G after Lawrence 1980; I by S. Monteith]

which may be produced in male to form a plate or paired tubercles or horns. Antennal club large and loose with well-developed, multipronged sensoria; maxillae with reduced lobes and fusiform palps; pronotum large, sometimes with anterior plate or paired horns in male; tibiae almost always lacking spurs and with spines along outer edge; fore tibia often with acute tooth or comb of spines at apex; ventrite 1 often with setose fovea in male. Larvae elongate, subcylindrical, lightly sclerotised with variable armature (usually paired, hook-like urogomphi) on T9 and pygopod-like 10th segment. Antennae very short, with long sensorium arising from near base of terminal segment; mandible often with acute, hyaline process at base; maxilla with reduced, subapical lacinial lobe. Most Ciidae feed as adults and larvae on the hyphae comprising the more durable fruiting bodies of various Basidio-

mycetes, particularly Polyporaceae; but some feed in rotten vines or branches. One Australian species, *Cis bilamellatus*, was introduced into Britain and is now generally distributed throughout England and southern Scotland (Hammond 1974; Paviour-Smith 1960). Most Australian species belong to *Cis*, but *Xylographus*, *Octotemnus* and *Orthocis* are also well represented. [Blair 1940; Lawrence 1973]

**89. Melandryidae** (Fig. 35.51c). ADULT: ANT 11 (FIL/SERR/INCR), FCOX TRANS-GLOB(CONC), FCAV OPEN(CLOS), MCOX CONT-NARR(OPEN), 5-5-4, ABD 5(2), 1.2-15 mm. LARVA: HEAD PRO (PRO)/HYPO, STEM 0/5, ANT 3, FSUT +, LABR FR, MOLA 0, VMP RET, MALA, MP 3, LP 2, HSC 0, HRD 0/+, VER 0, LEGS 5, TS 1/2, UROG +, SPIR AN/AU/AB.

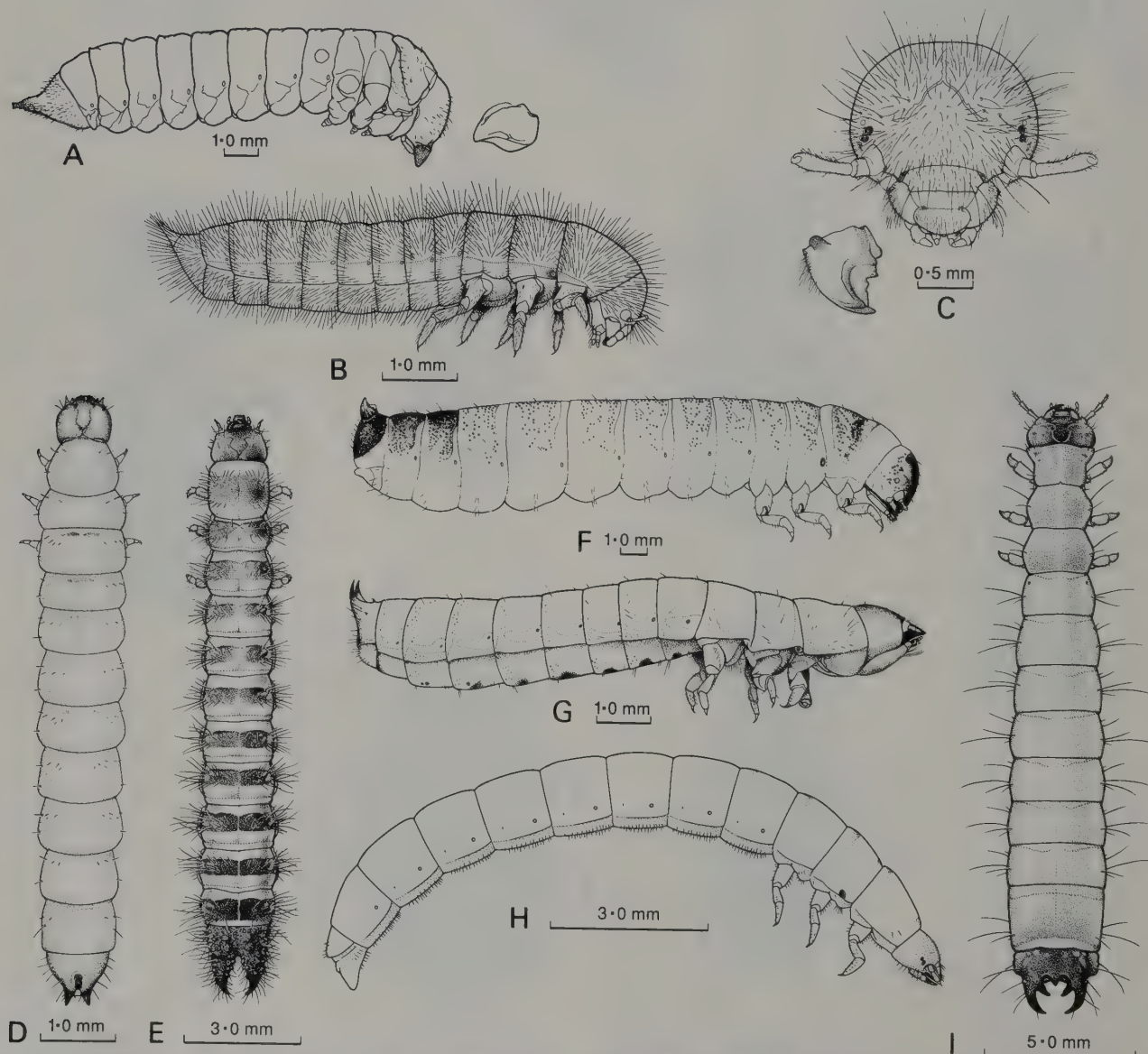


Fig. 35.52 Larvae of Tenebrionoidea: A, unidentified Mordellidae, lateral; B, *Ecnolagria grandis*, Tenebrionidae-Lagriinae, lateral; C, same, head and mandible, dorsal; D, *Pycnomerus* sp., Colydiidae, dorsal; E, *Meryx rugosa*, Zopheridae-Merycinae, dorsal; F, *Orcopagia monstrosa*, Tenebrionidae-Tenebrioninae, lateral; G, *Promethis nigra*, Tenebrionidae-Coelometopinae, lateral; H, *Scymena amphibia*, Tenebrioninae, lateral; I, *Morpholycus costipennis*, Pythidae-Pilipalpinae, dorsal. [A, C by A. Klinkenberg; B, H by F. Nanninga; D by A. Atkins; E, I by T. Nolan; F by A. Hastings; G by S. P. Kim]



Elongate beetles, usually more or less wedge-shaped (tapering posteriorly and more convex ventrally than dorsally), with vestiture of fine, decumbent hairs. Head deflexed, not abruptly constricted behind eyes and deeply inserted into prothorax; eyes vertical and at least slightly emarginate; antennal insertions exposed; maxillary palps variously modified, often with apical segment strongly expanded and securiform or cultriform; lateral pronotal carinae incomplete anteriorly; mid and hind tibiae often with a number of short combs, which may also be present at the apices of the tibiae and tarsal segments. Larvae elongate, usually subcylindrical and lightly sclerotised except for urogomphi, which may be minute. Head with long epicranial stem and coincident endocarina; antennae very short; stemmata never well developed; mandibles stout and symmetrical; malae simple and obtuse. Melandryid larvae occur in dead wood or in the more durable fruiting bodies of some Basidiomycetes. Adults are often active on surfaces at night, and those of the Orchesiini are capable of jumping. All Australian species belong to the MELANDRYINAE and most are currently placed in the genus *Orchesia*, which is probably a composite of several genera. Other common genera are *Callidircaea* and *Talayra*. The most unusual species is *Mystes planatus*, which has strongly flattened adults and very long, slender larvae which resemble those of Lymexylidae. [Champion 1916a, b; Crowson 1966b]

**90. Mordellidae** (Figs 35.51D, 52A). ADULT: ANT 11(FIL/SERR), FCOX PROJ(CONC), FCAV OPEN(CLOS), MCOX VWIDE(OPEN), 5-5-4, ABD 5(0), 1.5-15 mm. LARVA: HEAD HYPO, STEM 0/1-3, ANT 1-3, FSUT +, LABR FR, MOLA 0, VMP RET, MALA, MP 2/3, LP 2, HSC 0, HRD +, VER 0, LEGS 3/4, TS 0, UROG 0/+, SPIR AN.

Strongly wedge-shaped beetles, characteristically humped, laterally compressed and posteriorly tapered, with the last sclerotised tergite (7) produced, forming acute process extending well beyond elytral apices. Body clothed with fine, decumbent hairs; head strongly deflexed, concealing prosternum, fore and mid coxae, and abruptly constricted behind eyes to form narrow neck, which is concealed by abutment of head against pronotum; lateral pronotal carinae are complete; hind coxae very large; tibiae and tarsal segments often bear combs of spines; tarsal claws serrate or pectinate, each with bristle-like appendage beneath. Larvae (Fig. 35.52A) elongate, subcylindrical and very lightly sclerotised, with globular head, long epicranial stem and coincident endocarina, robust mandibles, short legs, which are indistinctly 3- or 4-segmented, without claws, and T9 often with pair of minute urogomphi or median terminal spine. Adults are often found on flowers and foliage, and when disturbed they usually tumble about by rapidly moving the hind legs. Larvae usually bore through rotten wood or mine the stems of various herbs, but a few occur in fungus fruiting bodies. Australian species belong to several genera, including *Tomoxioda*, *Mordella*, *Austromordella*, *Hoshihanania*, *Glipostenoda* and *Mordellistena*. [Ermisch 1962; Lea 1917b]

**91. Rhipiphoridae** (Figs 35.53A-D). ADULT: ANT

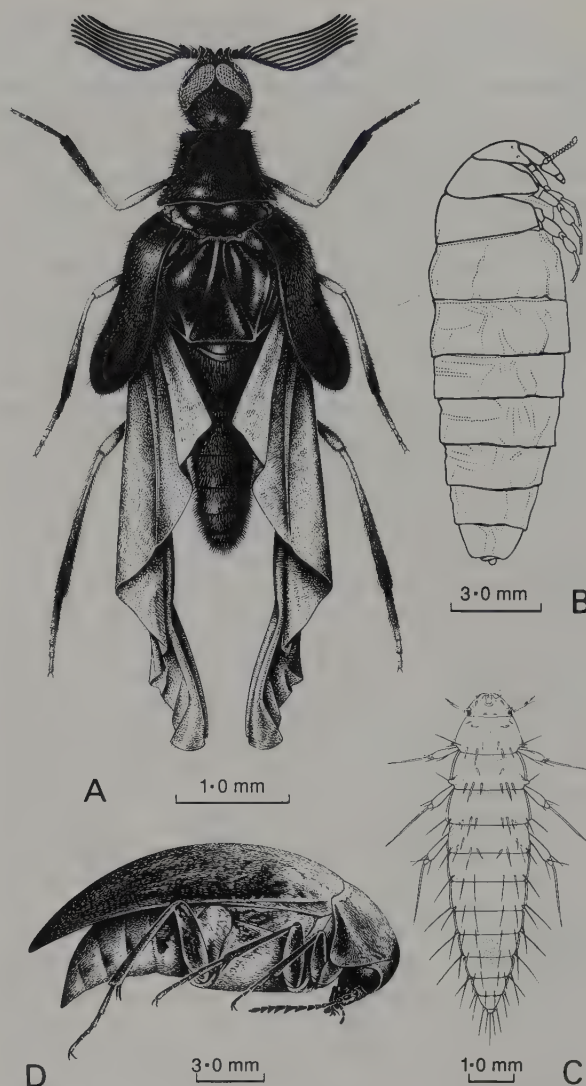


Fig. 35.53 Rhipiphoridae: A, *Rhipidioides rubricatus*, adult ♂; B, *Riekella australis*, adult ♀; C, *Rhipidioides helenae*, triungulin; D, *Trigonodera marmorata*, ♀. [F. Nanninga]

7R/11(FILR/SERR/PECT/FLAB/1R), FCOX PROJ (EXPr-CONC), FCAV OPEN(OPENR-CLOS), MXCOX CONT-MWIDE(OPEN), 5-5-4/4-4-4R, ABD 5-7/9R(0), 3.5-38 mm. LARVA: HEAD PRO(PRO)/HYPO, STEM 0/4/5, ANT 1-3, FSUT 0, LABR FU, MOLA 0, VMP RET/PRO, MALA, MP 1-3, LP 0/1, HSC 0, HRD 0, VER 0, LEGS 0/4/5, TS 0/2, UROG 0, SPIR AN/RED.

Elongate beetles, often laterally compressed and posteriorly tapered, as in Mordellidae, but without abdominal spine. Body often subglabrous or clothed with decumbent hairs; head may be strongly deflexed and abruptly constricted behind eyes to form neck, which may or may not be visible; eyes slightly to strongly emarginate and sometimes very large; elytra may be entire and slightly dehiscent, exposing the abdominal apex, or highly reduced exposing most of abdomen. Females of Rhipidiinae (Fig. 35.53B) lack both elytra and hind wings and have reduced mouth-parts. Known larvae are usually very lightly sclerotised parasitoids, but in Rhipiphorinae and Rhipidiinae



the 1st instars are minute, well-sclerotised triungulins (Fig. 35.53C). The Australian species are placed in 5 subfamilies. PELECOTOMINAE (Fig. 35.53D) and PTILOPHORINAE include the least specialised forms, in which the adults have complete elytra and minor sexual dimorphism and the larvae are probably predators or ectoparasitoids of wood-boring larvae; *Trigonodera* is included in the former group, *Ptilophorus* in the latter. In HEMIRHIPIDIINAE (*Nephrites* and *Sitarida*), the antennal dimorphism is slight but the elytra are abbreviated; larvae are not known, but *S. scabriceps* was reared from a beetle-infested *Acacia* log. In RHIPIPHORINAE, the male antennae are biflabellate, while those of the female are pectinate, and the elytra are either dehiscent and more or less acute at apex (*Macrosiagon*) or very short (*Rhipiphorus*). Rhipiphorines lay their eggs in flowers, on the undersides of leaves or in soil, and the 1st instar triungulins attach themselves to solitary bees (*Rhipiphorus*) or wasps of the families Vespidae, Sphecidae, Tiphidae or Scolidae (*Macrosiagon*). These minute larvae enter the nest with the female and eventually bore into the hymenopteran larvae. This endoparasitic phase is followed by an ectoparasitic one, in which the larva leaves the body of the host and feeds externally. In RHIPIDIINAE, the male (Fig. 35.53A) is small and midge-like, with very short elytra and large eyes; the female (Fig. 35.53B) is larviform, without elytra or hind wings. Rhipidiine triungulins attach themselves to cockroach nymphs, pierce the cuticle and feed externally for a short time, and then bore into the host to become endoparasitic. *Riekella* are parasites of Blattidae, *Paranephrites xenus* has been reared from Blaberidae, and all other genera, including *Rhipidioides*, have been associated with Blattellidae. [Besuchet 1956a; Callan 1981; G. V. Hudson 1934; Linsley *et al.* 1952; Riek 1955a, 1973b; Selander 1957]

**92. Colydiidae** (Figs 35.51F, G, 52D). ADULT: ANT 10–11 (INCR<sub>R</sub>/1–3), FCOX GLOB(CONC), FCAV OPEN–CLOS(OPEN), MCOX NARR–VWIDE(CLOS), 4-4-4/3-3-3A, ABD 5(0/3/4), 1.1–9 mm. LARVA: HEAD PRO(PRO), STEM 0/5, ANT 3, FSUT 0, LABR FR, MOLA 0r/+, VMP RET, MALA, MP 3, LP 1r/2, HSC 0/+, HRD 0/+, VER 0, LEGS 5, TS 2, UROG 0r/+, SPIR AB.

Narrowly elongate to oblong or ovate and strongly convex to flattened, usually brown or black in colour, and subglabrous or variously clothed with decumbent or erect hairs, bristles or scales. Antennal insertions concealed; usually with well-developed frontoclypeal ridge which may be produced forward; lateral pronotal carinae almost always complete and often crenulate or dentate; prosternal process flat and not or only slightly expanded apically; tarsi almost always simple; articulations between ventrites usually similar, so that all ventrites lie on same plane. Larvae (Fig. 35.52D) elongate, cylindrical to somewhat flattened, and relatively lightly sclerotised, except for head and T9, the latter almost always with pair of urogomphi and often a sclerotised pit between them. Colydiidae are common under bark, in rotten wood and in leaf litter, and most appear to be mycophagous. Some are associated with moss or lichens, and others feed on the

fruiting bodies of pyrenomycetous fungi (Ascomycetes). *Todima* are found in the leaf bases or on the flower stalks of grass trees (*Xanthorrhoea*). The Papuan *Pseudendestes robertsi* is known to prey on the larvae of platypodine weevils, and it is likely that the Australian *P. australis* has similar habits. Some of the more common Australian genera are *Pycnomerus*, *Ablabus* and *Sparactus*. *Dryptops* are particularly interesting in that they harbour an epicuticular growth of cryptogams, giving them a green colour (Samuelson 1966). [Carter and Zeck 1937; Lawrence 1980; Ślipiński 1987b]

**93. Monommidae.** ADULT: ANT 11(3), FCOX GLOB(CONC), FCAV OPEN(OPEN), MCOX VWIDE(CLOS), 5-5-4, ABD 5(0), 6 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT 0, LABR FR, MOLA 0, VMP RET, MALA, MP 3, LP 2, HSC 0, HRD +, VER 0, LEGS 5, TS 2, UROG +, SPIR AB.

Ovate beetles, moderately convex above and below, black in colour and subglabrous. Eyes very large and subcontiguous dorsally; antennal insertions concealed and antennae housed in grooves in hypomera; elytral epipleura are moderately broad and complete; elytral punctation is seriate; first 2 or 3 tarsal segments densely pilose beneath; last ventrite with a deep, curved, transverse groove. Larvae elongate, parallel sided and somewhat flattened with widely separated urogomphi with a broad pit between them. Paired endocarinae located between frontal arms; mandible bears row of hyaline teeth in molar region; mala is truncate and cleft; and T2 to T6 or T7 each have a double row of asperities forming an incomplete transverse ring on each side of the midline. The only known Australian species, *Monomma australe*, is known only from the holotype, which has no definite type locality (Freude 1955); it is closely related to the Indian *M. brunneum*, the larvae of which are known to feed in the rotten stems of pawpaw (Fletcher 1916).

**94. Zopheridae** (incl. Merycidae; Figs 35.51H–J, 52E). ADULT: ANT 11(FIL<sub>R</sub>/2–3), FCOX GLOB–PROJR(CONC), FCAV OPEN<sub>R</sub>/CLOS(OPEN), MCOX NARR–VWIDE(OPEN–CLOS), 5-5-4/4-4-4R, ABD 5(3), 1.8–35 (2.5–8) mm. LARVA: HEAD PRO(PRO), STEM 0/3/5, ANT 3, FSUT 0/+, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0/+, VER 0/+, LEGS 5, TS 0/2, UROG +, SPIR AB.

Elongate and parallel sided, or more oblong with elytra much broader at base than prothorax, and usually clothed with decumbent and/or erect setae, bristles or scales (rarely subglabrous). Upper surfaces often tuberculate or ridged; vestiture may form a pattern; antennal insertions usually exposed; antennal club usually weak and sometimes not clearly visible because of bristles or scales clothing most antennal segments; prosternal process more or less abruptly expanded apically, closing or almost closing coxal cavities from behind; elytral epipleura complete; tarsi not lobed. *Meryx* differs from other zopherids in having only 4 segments in the fore and mid tarsi, and *Zopherosis georgei* is much larger (more than 25 mm) than the remainder of the group. Larvae elongate, subcylindrical to slightly flattened, and usually lightly sclerotised except for head and abdominal apex (in *Meryx*



there are pigmented plates on all thoracic and visible abdominal segments); T9 and occasionally other terga may bear tubercles of various sizes or sclerotised ridges. Epicranial stem short to moderately long; mandibles more or less symmetrical with reduced mola; cardines are usually divided internally; mala obtuse and cleft; frontoclypeal suture absent, except in *Dipsaconia*, which has short, diverging hypostomal rods. The family is represented in Australia by the ZOPHERINAE (*Zopherosis*), ULODINAE (*Ulodes*, *Dipsaconia*, *Ganyme*, *Phaennis*, *Notocerastes*), PARAHELOPINAE (*Melytra*) and MERYCINAE (*Meryx*), and also by the genera *Latometus*, *Docalis* and *Cotulades*, which are tentatively placed in this family but appear to have more in common with some Colydiidae (Sarotriini). Adults and larvae of Ulodinae are known to feed on the soft fruiting bodies of certain Basidiomycetes, such as *Piptoporus* (Polyporaceae) and *Pleurotus* (Tricholomataceae). Adult *Zopherosis* may feed externally on fungi, and those of *Cotulades* and *Latometus* may feed on lichens at night; larvae of the last two have been collected in white, rotten wood. Adults and larvae of *Meryx rugosa* have been collected under the bark of fungus-infested logs. [Doyen and Lawrence 1979]

**95. Chalcodryidae** (Fig. 35.54A). ADULT: ANT 11(3), FCOX PROJ(CONC), FCAV CLOS(OPEN), MCOX NARR(OPEN), 5-5-4, ABD 5(3), 10-17 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT +, LABR FR, MOLA 0, VMP RET, MALA, MP 3, LP 3, HSC 0, HRD 0, VER 0, LEGS 5, TS 2, UROG +, SPIR AM.

The only Australian genus currently placed in this family is *Sirrhas*, which includes elongate, somewhat flattened, relatively soft-bodied forms with long legs and long, slender, weakly clubbed antennae. Antennal insertions exposed; apical segment of maxillary palp securiform; eyes slightly emarginate; prosternal process narrow and abruptly expanded apically as in Zopheridae; tarsi not lobed. Larvae elongate, parallel sided and slightly flattened, with dorsal surfaces well sclerotised and distinctively marked with yellow and brown; antennae moderately long; epicranial stem long; T9 with ring of 10 acute processes, the apical 4 of which represent the forked urogomphi. Both adults and larvae have been found by beating or pyrethrin spraying the crowns of tree ferns in Tas. The inclusion of *Sirrhas* in this family is open to question, since both adults and larvae have a number of features in common with both Zopheridae and Perimylopidae (from southern South America), while the larvae differ in several respects from those of the New Zealand *Chalcodrya*. [Watt 1967, 1970, 1974a]

**96. Tenebrionidae** (incl. Alleculidae, Lagriidae, Nilionidae; Figs 35.52B, C, F-H, 54B-G; Plates 4, C, 5, E). ADULT: ANT 3R/8R/10R/11(FIL/MON/INCR/1R/2R/3/4R/6-7), FCOX TRANS/GLOB/PROJ(CONC), FCAV OPENR/CLOS(OPENR/CLOS), MCOX NARR-VWIDE(OPEN-CLOS), 5-5-4/4-4-4R, ABD 5(3), 1.5-36 (2.5-25) mm. LARVA: HEAD PRO(PRO)/HYPO, STEM 0-5, ANT 1-3, FSUT +, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 1R/2, HSC 0R/+, HRD 0, VER 0/+, LEGS 5, TS 2, UROG 0/+, SPIR AN/AM.

Highly variable in form, but usually black or brown

and subglabrous, with concealed antennal insertions and usually stout, moniliform or incrassate antennae. Eyes usually emarginate; lateral pronotal carinae usually simple and complete; prosternal process usually moderately broad, strongly curved dorsally behind coxae, neither strongly nor abruptly expanded apically; junctions of first 3 ventrites different from those separating last 2, the basal ventrites being strongly connate and the apical ones more or less movable, often with exposed membrane. Externally open fore coxal cavities occur only in *Tanylypa*, internally open ones in some Tenebrioninae. Although almost all species have a 5-5-4 tarsal formula, reduction to 4-4-4 has occurred at least 7 times in Australian tenebrionids (usually in small and relatively rare species). Most members of the family are also characterised by having paired glandular reservoirs, associated with a chemical defence system, located usually at the base of the 5th ventrite. In some Adeliini, these reservoirs are completely extruded when the animal is disturbed. Most Lagriinae and Alleculinae differ from other tenebrionids in having a distinctly lobed penultimate tarsal segment, and the latter are further distinguished by their pectinate tarsal claws. Larvae (Figs 35.52B, C, F-H) are almost always elongate (ovate in Leiochrini) and subcylindrical to slightly flattened. They may be very lightly sclerotised, moderately sclerotised and yellow in colour, with or without darker head and urogomphi, or uniformly heavily sclerotised and darkly pigmented; and the vestiture consists of scattered, fine hairs, except in Lagriini, whose larvae are densely setose. Some are called 'false wireworms' because of their resemblance to elaterid larvae, but they have a very different type of head, which is less flattened and with a distinct clypeus and labrum. A combination of frontoclypeal suture, simple and rounded mala, and no hypostomal rods will distinguish tenebrionid larvae from those of most related groups.

Tenebrionids are primarily scavengers, feeding on a variety of dead material of plant or fungal (rarely animal) origin, and they have been able to survive better than most beetles in arid habitats throughout the world. Many (mainly Lagriini, Adeliini, Heleini and Opatrini) occur under rocks and in leaf litter, with the larvae living in the soil or scavenging on the ground at night; among these are a number of psammophilous species (*Sphargeris physodes*, *Trachyscelis*, Heterocheirini, Hyociini, some Opatrini) occurring on dunes or near accumulations of debris along ocean beaches or on sandy river banks. A number of tenebrionid larvae (some Adeliini, Phrenapatinae, *Tanylypa*, *Meneristes*, *Asphalus*, many Cyphaleini, Ulomini, some Amarygmini, Alleculinae, Gnathidiini and Coelometopinae) feed in rotten wood; adults may also feed on the wood (Ulomini, Gnathidiini), but more often they occur on surfaces at night feeding on lichens, fungi or plant material. Some larval forms may also graze on surfaces at night; these are known in *Titaena*, *Amarygmus* and the Leiochrini. Members of the Toxicini and Bolitophagini and most Diaperini feed as both larvae and adults on fungal fruiting bodies (particularly Polyporaceae), while other tenebrionids may occur in caves (*Brises*) or animal nests. Some subterranean

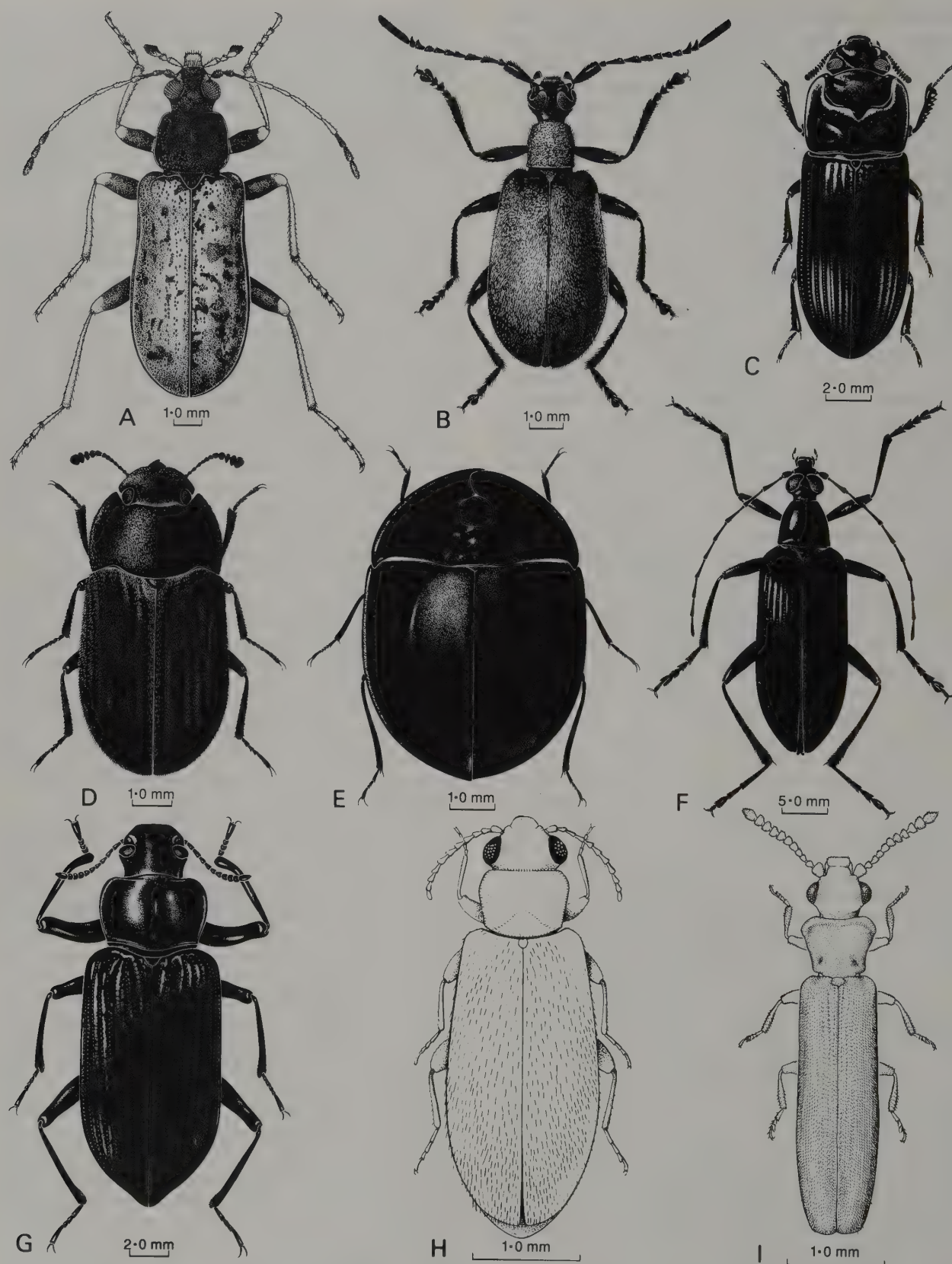


Fig. 35.54 Tenebrionoidea: A, *Sirrhias* sp., Chalcodryidae; B–G, Tenebrionidae: B, *Ecnolagria grandis*, Lagriinae; C, *Achthosus westwoodi*, Tenebrioninae; D, *Gonocephalum meyricki*, Tenebrioninae; E, *Heleus waitei*, Tenebrioninae; F, *Tanychilus striatus*, Alleculinae; G, *Promethis nigra*, Coelometopinae; H, *Trichosalpingus brunneus*, Mycteridae-Laconotinae; I, *Hemipeplus australicus*, Mycteridae-Hemipeplinae.

[A by A. Hastings; B–H by F. Nanninga; I by S. Monteith]



forms will feed on the roots of plants, including commercial crops; these false wireworms occur in several genera, including *Celibe*, *Pterohelaus*, *Isopteron* and *Gonocephalum*. A number of species (known as mealworms and flour beetles) have become serious pests of stored products; these include *Alphitobius diaperinus*, *A. laevigatus*, *Gnatocerus cornutus*, *Latheticus oryzae*, *Palorus subdepressus*, *Tenebrio molitor*, *T. obscurus*, *Tribolium castaneum* and *T. confusum*. The Egyptian beetle (*Blaps polychresta*) was accidentally introduced from North Africa, and has become relatively common in S.A. around human habitations; however it is not considered a pest species.

All of the 7 subfamilies recognised by Doyen *et al.* (1990) occur in Australia. LAGRIINAE (37 genera) includes Adeliini, a dominant group in forested areas but not common in the dry interior, Goniaderini, Lupropini, Lagriini (formerly the Lagriidae), Cossyphini, Belopini and Chaerodini (*Sphargeris*). PHRENAPATINAE includes *Archaeoglenes* and the Penetini (4 genera); while PIMELIINAE is comprised of several rare groups of doubtful affinities (e.g. *Tanylypa* in Zolodiniini, Cnemeplatiini, Ceratanisini) plus an introduced *Ocnera* (Pimeliini). TENEBRIONINAE (90 genera) contains the bulk of the tribes, including Toxicini, Bolitophagini, Tenebrionini, Heleini, Cyphaleini, Titaenini, Alphitobiini, Triboliini, Ulomini, Heterocheirini, Opatrini, Leichenini, Amarygmini and the introduced Blaptini. ALLECULINAE and DIAPERINAE each include 25 genera, and the latter includes Crypticini, Phaleriini, Trachyscelini, Myrmexchixenini, Hypophloeini, Gnathidiini, Hyociini, Ectychini, Leiochrini, Scaphidemini and Diaperini. COELOMETOPINAE (22 genera) includes Coelometopini and Strongyliini. *Adelium* and *Cardiothorax* are the largest adeliine genera. *Tanylypa morio* from Tas. is a very

unusual and probably primitive species most closely related to the New Zealand *Zolodinus zelandicus*. The Heleini include the strongly flattened and wingless 'pie-dish beetles', which are most common in the dry interior of the continent, as well as the genus *Lepispilus*, larvae of which occur in rotten wood. The related Cyphaleini include many brightly coloured, metallic forms, like *Prophanes mastersi*, as well as the dark coloured and heavily sclerotised, xerophilous species belonging to *Nyctozeilus* and related genera. The large amarygmene genus *Chalcopteroides* includes a number of species which are metallic blue or green with an iridescent sheen. [H. J. Carter 1926; Doyen 1966, 1984, 1985; Doyen and Lawrence 1979; Doyen and Tschinkel 1982; Doyen *et al.* 1990; Tschinkel and Doyen 1980; Watt 1974b]

**97. Prostomidae** (Fig. 35.55A). ADULT: ANT 11(3), FCOX GLOB(CONC), FCAV CLOS(CLOS), MCOX MWIDE(CLOS), 4-4-4, ABD 5(2), 5-10 mm. LARVA: HEAD PRO(PRO), STEM 0, ANT 3, FSUT 0, LABR FR, MOLA +, VMP PRO, MALA, MP 3, LP 2, HSC +, HRD +, VER 0, LEGS 5, TS 2, UROG +, SPIR AB.

Elongate, more or less parallel-sided, flattened, reddish brown and subglabrous beetles. Head either elongate with large, projecting mandibles (*Prostomis*) or expanded laterally and wider than pronotum (*Dryocora*); genae slightly to strongly produced anteriorly; eyes small; frontoclypeal suture distinct; lateral pronotal carinae absent; fore and mid coxae widely separated. Larvae elongate, parallel sided, flattened and lightly sclerotised, with broad, asymmetrical head; mandibles with large, asymmetrical, transversely ridged molae; mala rounded and broadly cleft; T9 with pair of lightly sclerotised, slightly upturned urogomphi; S9 with row of fine asperities at apex. Adult and larval prostomids occur within wet, brown rotten wood, and their presence is marked by

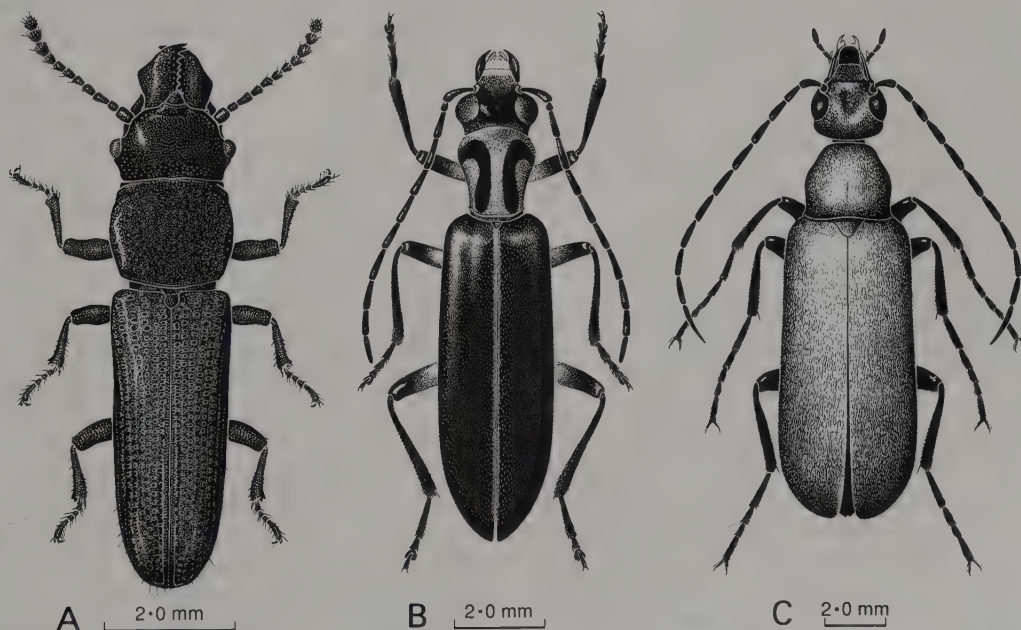


Fig. 35.55 Tenebrionoidea: A, *Prostomis atkinsoni*, Prostomidae; B, *Thelyphassa mira*, Oedemeridae; C, *Zonitis lutea*, Meloidea.

[A by S. Monteith; B, C by F. Nanninga]

the mud-like consistency of the substrate. *Prostomis* occurs throughout eastern Australia and also in western North America, eastern Asia, Africa and the Pacific region, whereas *Dryocora* is known from Vic., Tas. and New Zealand only.

**98. Oedemeridae** (Fig. 35.55B). ADULT: ANT 11(FIL/SERR/INCR), FCOX PROJ(EXP), FCAV OPEN(CLOS), MCOX CONT(OPEN), 5-5-4, ABD 5/6(2), 2.5–26 (7–18) mm. LARVA: HEAD PRO(PRO), STEM 0/2/5, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0, VER 0, LEGS 5, TS 2, UROG 0, SPIR AN/AM.

Elongate, parallel-sided and soft-bodied beetles, often bicoloured and clothed with short, decumbent hairs. Head usually somewhat produced anteriorly; antennal insertions located dorsally in front of eyes; lateral pronotal carinae absent; apical segment of the maxillary palp more or less expanded and truncate (excavate in some males); penultimate tarsal segment lobed beneath. Larvae elongate, subcylindrical and very lightly sclerotised, with large, often slightly asymmetrical head and asperity-bearing ampullae on T1–T2 or T1–T3 and S2–S4 or S3–S4. Antennae well developed; epicranial stem long and frontal arms V-shaped; mandibles large and asymmetrical, with transversely ridged molae; ligula well developed, with prehypopharyngeal lobe between it and hypopharynx. Oedemerid larvae feed in dead wood, and they are most common in that which has undergone white rot. Adults occur in flowers or on foliage and may be beaten from vegetation by day or collected at lights at night; at least some species feed on pollen, which may be stored in the large crop, but fungal spores and even pieces of cuticle are sometimes found in the gut. Some oedemerids are known to contain cantharidin, and several are aposematically coloured and form part of mimicry complexes (Moore and Brown 1989). The subfamily NACERDINAE is represented in Australia by the cosmopolitan *Nacerdes melanura*, whose larvae damage wharves and other marine structures, and by *Agasma semicrudum*, whose nearest relatives are species of the Holarctic genus *Ditylus*. The remaining species belong to the Asclerini (OEDEMERINAE). *Pseudolycus* is black and orange and mimics *Metriorrhynchus* and certain other Lycidae. [L. Hudson 1975; Lea 1917a, b; Švihla 1986]

**99. Meloidae** (Fig. 35.55C; Plate 6, B). ADULT: ANT 11(FIL/SERR), FCOX PROJ(EXP), FCAV OPEN(OPEN), MCOX CONT(OPEN), 5-5-4, ABD 6(0), 7–25 (7–18) mm. LARVA: HEAD PRO(PRO)/HYPO, STEM 0–2, ANT 1/3, FSUT 0/+, LABR FR/FU, MOLA 0, VMP PRO, MALA, MP 0r/3, LP 0r/1/2, HCS 0, HRD 0, VER 0, LEGS 0r/3r/5, TS 0–2, UROG 0, SPIR AN.

Elongate, moderately convex, soft-bodied beetles, often bicoloured with red or yellow and black or blue, but sometimes uniformly red or metallic blue or violet. Body subglabrous or clothed with short, decumbent hairs; head strongly constricted behind eyes to form narrow neck; prothorax usually narrowed anteriorly and lacks lateral carinae; tarsal claws pectinate with a blade-like process beneath each claw. Larvae are of three types: 1) a minute, fusiform, well-sclerotised triungulin with long legs; 2) a

grub-like, ectoparasitic larva, lightly sclerotised, with short legs and a hypognathous head; and 3) a coarctate form with reduced mouth-parts and appendages. Australian meloids belong to the subfamilies HORIINAE (*Horia mira*) and ZONITINAE (*Palaestra*, *Zonitis*), all of which are parasitoids of bees (HYMN: Apoidea). Eggs are laid on flowers, and the active triungulins attach themselves to bees in order to gain access to the nest. Later instars consume both bee larva and provisions of honey and nectar. The coarctate larva is a resting stage, which gives rise to another grub-like prepupal form. [Kaszab 1969; Kifune 1961]

**100. Mycteridae** (incl. Hemipeplidae; Figs 35.54H, I). ADULT: ANT 11(FIL/SERR), FCOX PROJ(CONC), FCAV OPEN(CLOS), MCOX NARR(CLOS), 5-5-4, ABD 5(2/4), 2.2–7.7 mm. LARVA: HEAD PRO(PRO), STEM 5, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET/PRO, MALA, MP 3, LP 1, HSC 0, HRD +, VER 0, LEGS 5, TS 2, UROG +, SPIR AN/AM.

Elongate to narrowly elongate and slightly to strongly flattened beetles, yellow to brown and clothed with small to minute, decumbent hairs. Eyes prominent and non-emarginate; lateral pronotal carinae absent; and at least the penultimate tarsal segment lobed beneath. Except in *Hemipeplus*, which is narrowly elongate, strongly flattened and yellow in colour, the mesepisterna meet at the midline and there is a densely pubescent secretory patch on ventrite 2 in the male. Larvae elongate, parallel sided, strongly flattened and lightly sclerotised, with broad head and an articulated, terminal plate formed by T9. Head without median endocarina (except in *Hemipeplus*); mandibular molae usually reduced and sub-basal; legs short and widely separated; with paired rows of asperities forming incomplete rings on T2–T6 and S2–S6; S9 forms distinctive U-shaped sclerite, enclosing segment 10. Mycterid larvae occur under bark of trees or in leaf axils or dead fronds of various monocotyledonous plants. The Australian fauna includes *Hemipeplus australicus* (HEMIPLELINAE), which breeds in the leaf axils of *Lomandra banksii* (Xanthorrhoeaceae) and the LACCONOTINAE, most of which belong to *Trichosalpingus*. *Loboglossa australica* is our largest species, with close relatives in Chile. [Champion 1916b; Crowson and Viedma 1964; Thomas 1985]

**101. Pythidae** (incl. Pilipalpidae; Figs 35.52I, 56A–C). ADULT: ANT 11(FIL/MON/SERR/PECT), FCOX PROJ(EXP–CONC), FCAV OPEN(OPEN), MCOX CONT–NARR(OPEN), 5-5-4, ABD 5(0/2), 3.8–14 mm. LARVA: HEAD PRO(PRO), STEM 2/5, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0/+, VER 0/+, LEGS 5, TS 2, UROG +, SPIR AN/AB.

Elongate, moderately convex to somewhat flattened beetles, black, dark brown, or bicoloured with various combinations of red and black, and usually clothed with decumbent and erect hairs (subglabrous in *Synercticus*). Eyes prominent and not emarginate; head gradually narrowed behind eyes (not abruptly constricted); maxillary palps relatively small, usually expanded and truncate apically; lateral pronotal carinae absent or indistinct; tarsal



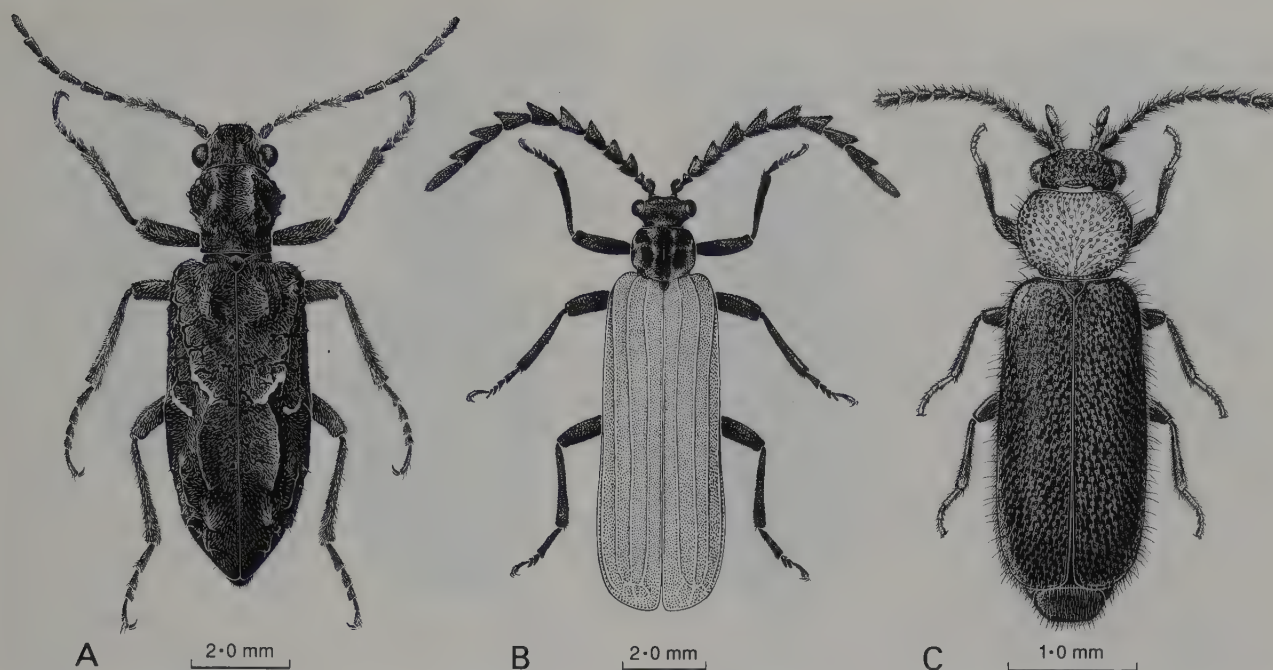


Fig. 35.56 Pythidae: A, *Anaplopus tuberculatus*, Anaplopinae; B, *Morpholycus costipennis*, Pilipalpinae; C, *Temnopalpus bicolor*, Pilipalpinae. [S. Monteith]

segments either simple or with penultimate and antepenultimate segments lobed beneath. Larvae (Fig. 35.52i) elongate, parallel sided, and more or less uniformly yellow (*Synercticus*) or with head and T9 darker in colour. Head broad; antennae relatively long; legs widely separated; T9 with pair of complex urogomphi (forked or with accessory processes) and usually additional armature; S9 with basal row of asperities, either slightly curved (Pilipalpinae) or strongly, doubly curved (*Synercticus*). Known larvae occur under the bark of rotten logs. As presently defined, the Pythidae in Australia include three distinct groups: *Synercticus*, which appears to be most closely related to the Holarctic Pythinae, *Anaplopus tuberculatus* (ANAPLOPINAЕ), which is tentatively placed in this family, and the PILIPALPINAЕ, primarily a Southern Hemisphere group with several genera in Chile, Madagascar and New Zealand and one in Japan. Australian pilipalpins are placed in *Morpholycus*, *Paromarteon*, *Temnopalpus* and *Techmessa*. [Lawrence 1987b; Watt 1987]

**102. Salpingidae** (incl. Dacoderidae, Inopeplidae, Othniidae, Tretothoracidae; Figs 35.57A–E). ADULT: ANT 10R/11(FILR/MONR/3), FCOX TRANSr/GLOB (CONC), FCAV OPEN/CLOSr(CLOS), MCOX CONT-VWIDE(CLOS), 5-5-4/4-4-4R, ABD 5(0/2), 1.4–11 (2.2–6) MM. LARVA: HEAD PRO(PRO), STEM 0/2/5, ANT 3, FSUT 0, LABR FR, MOLA 0/+, VMP RET, MALA, MP 3, LP 2, HSC 0/+, HRD +, VER 0/+, LEGS 5, TS 2, UROG +, SPIR AN/AU/AB.

Elongate, slightly to strongly flattened beetles, which are subglabrous or clothed with scattered setae (except in *Elacatis* which is densely clothed with decumbent hairs). Head prognathous, sometimes produced and rostrate, and never abruptly narrowed behind eyes; lateral pronotal

carinae complete, incomplete or occasionally absent, and simple, undulate or dentate; elytra rarely (*Inopeplus*) abbreviated, exposing several abdominal tergites; tarsi almost always simple; fore and mid tarsi 4-segmented only in *Aglenus* and *Ocholissa*. Larvae elongate, parallel sided, slightly to strongly flattened, and moderately to lightly pigmented, except for head and abdominal apex. Epicranial stem absent; frontal arms with relatively narrow angle between them and usually with paired endocarinae beneath them; hypostomal rods moderately to very long and subparallel; S9 with 1 to several teeth on each side at base (sometimes forming basal row interrupted at middle); except in a few Salpinginae, armature on T9 complex, with accessory processes on urogomphi and/or additional spines or processes in front of or between them. Adult salpingids are usually found on foliage or flowers, and larvae commonly occur under bark or in dead twigs, stems or vines, where they feed on bark or phloem (Howden and Howden 1981). Some exotic species have been reported to be predacious; the European *Sphaeriestes mutilatus* feeds on fruiting bodies of *Cucurbitodithis* (Ascomycetes: Pleosporales) (J. Franz 1955); and the subantarctic and northern Pacific AEGIALITINAE apparently feed on algae growing on intertidal rocks (Spilman 1967).

Australian Salpingidae belong to 6 of the 7 known subfamilies, several of which are usually given family status. DACODERINAE are represented by the unusual myrmecophilous species *Tretothorax cleistostoma* (Fig. 35.57D); AGLENINAE by the introduced, blind *Aglenus brunneus*, which is found in decaying vegetation; OTHNIINAE by *Elacatis delusa* (Fig. 35.57A), known also from Borneo and Papua New Guinea (Brooks 1965); and INOPEPLINAE by several species of *Inopeplus* (Fig. 35.57E). PROSTO-

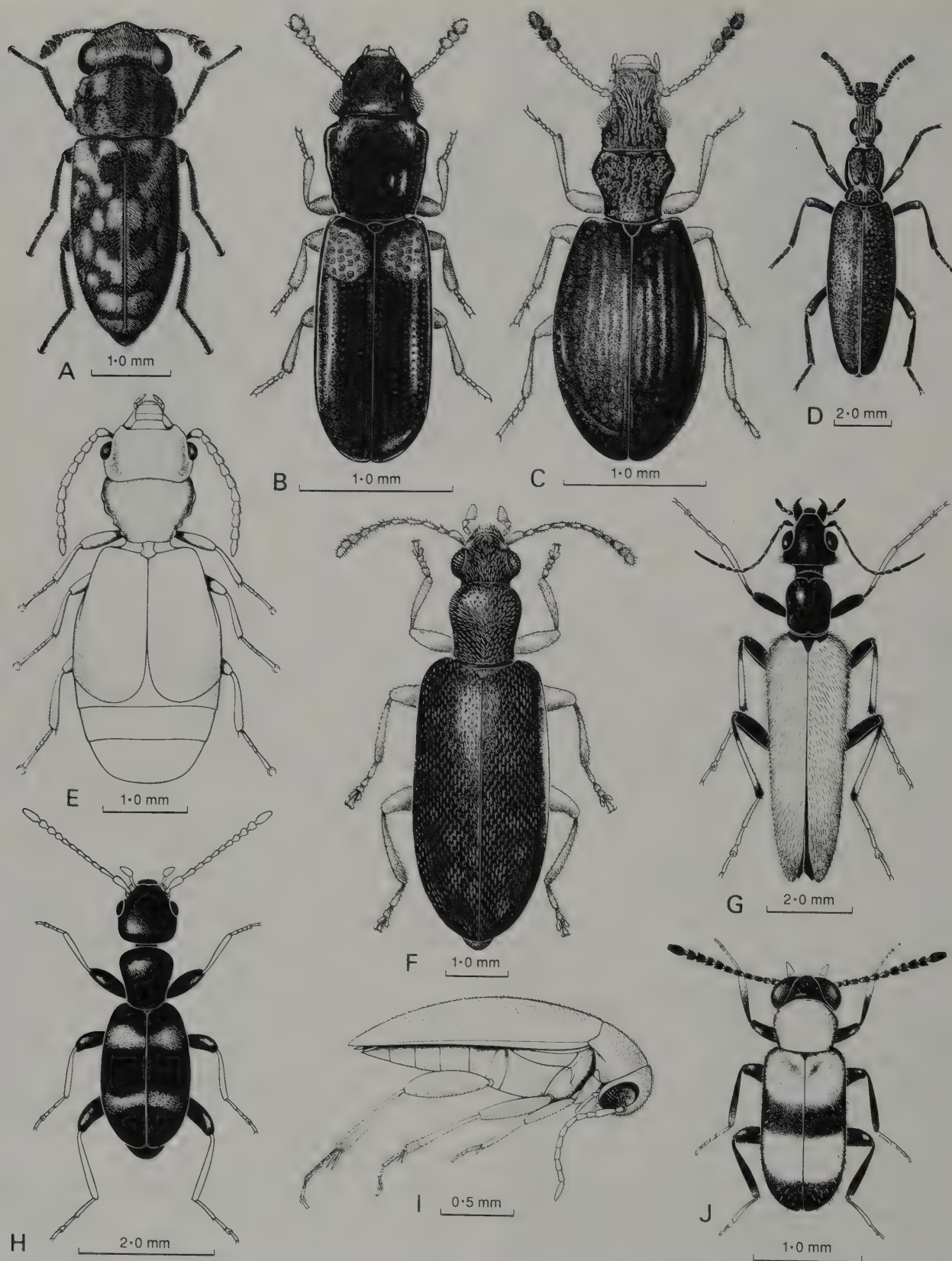


Fig. 35.57 Tenebrionoidea: A-E, Salpingidae: A, *Elacatis delusa*, Othniinae; B, *Ocholissa humeralis*, Prostominiinae; C, *Neosalpingus hybridus*, Salpinginae; D, *Tretothorax cleistostoma*, Dacoderinae; E, *Inopeplus dimidiatus*, Inopeplinae; F-H, Anthicidae: F, *Lagrioida australis*, Lagrioidinae; G, *Egestria taeniata*, Eurygeniinae; H, *Anthicus australis*, Anthicinae; I, *Scaptia australis*, Scaptiidae; J, *Syzeton abnormis*, Aderidae.

[A by S. P. Kim; B, C, F by A. Hastings; D, E, G-J by F. Nanninga]



MINIINAE are primarily tropical and include genera often placed in various other families; the Australian fauna includes *Ocholis* (Fig. 35.57B), *Prostomia* and *Szekessya*, as well as undescribed genera. SALPINGINAE are best represented in temperate regions; *Notosalpingus*, *Neosalpingus* (Fig. 35.57C), *Orphanotrophium*, *Lissodema* and *Platysalpingus* occur in Australia. [Blair 1919, 1925; Lawrence 1977, 1982; Sasaji 1988; Spilman 1954; Watt 1967]

**103. Anthicidae** (Figs 35.57F–H; Plate 5, D). ADULT: ANT 11(FIL/MON/INCR/3R), FCOX PROJ (CONC), FCAV OPEN–CLOS(CLOS), MCOX CONT–NARR (OPEN), 5-5-4, ABD 5/6(0/2R), 1.2–6.9 mm. LARVA: HEAD PRO(PRO), STEM 1/5R, ANT 3, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0/+, VER 0, LEGS 5, TS 2, UROG 0/+, SPIR AN/AB.

Elongate beetles, which are black, brown, yellow or red, sometimes bicoloured, and almost always clothed with decumbent and/or erect hairs. Antennal club, if present, very weak; except in *Lagrioida*, head abruptly constricted behind eyes to form neck and antennal insertions exposed; eyes not or only slightly emarginate; apical segment of maxillary palp slightly to strongly expanded apically and often securiform or cultriform; pronotum without lateral carinae, almost always constricted at middle, near base, or at base and apex; mesepisterna meet or almost meet at midline; penultimate tarsal segment lobed beneath; and first 2 ventrites free, except in *Lagrioida*. Larvae elongate, parallel sided, and lightly sclerotised or, in *Lemodes*, with dark and light pattern dorsally. Antennal sensorium usually broad and dome-like; with single pair of well-developed stemmata, except in *Lagrioida* (which has 5); with median endocarina in Anthicinae; mandibular mola usually reduced and sub-basal; mala usually simple (cleft in *Lagrioida*); S9 usually simple (with 2 basal teeth in *Lagrioida*); urogomphi, if present, often with accessory mesal processes near base; segment 10 more or less transverse and posteroventrally oriented.

Anthicids are usually found in decaying vegetation and leaf litter, and some may be common in beach drift or on sand dunes in arid regions. They are thought to be general scavengers, and some exotic forms have been reported to feed on egg masses or fly puparia. *Lagrioida australis* (LAGRIOIDINAE) is widely distributed on beaches along the east coast, and related species occur in New Zealand and Chile. The genus differs from all other anthicids in a number of adult and larval features, and it may be misplaced in this family. *Macratia* (MACRATRIINAE) is a world-wide genus with several species extending into Australia. EURYGENIINAE are well represented with 6 genera, 2 of which (*Ictistygna* and *Egestriomima*) differ from other members of the family in having closed fore coxal cavities. Little is known of eurygeniine biology, and the only known larva is of a Nearctic species. LEMODINAE are an endemic group which may be related to the Holarctic Ischaliinae (often placed in Pyrochroidae). *Lemodes* (Plate 5, D) and the related *Lagriomorpha* from Papua New Guinea are noted for their spectacular red or red and blue colour. *Lemodes* larvae were found in cells in wood,

where they had been deposited by a predatory wasp; the bicoloured pattern on the dorsal surface of the larva suggests that it feeds on surfaces. The related *Trichananca* are common in leaf litter, and their larvae are distinguished by lacking urogomphi. The largest group is the ANTHICINAE, which also includes the smallest species. Among these are species of *Mecynotarsus*, which have the pronotum produced into a horn-like process over the head. Other genera include *Anthicus*, *Formicomus* and *Tomoderus*. *Anthicus floralis* is a cosmopolitan species which occurs in foodstuffs. [Abdullah 1969; Armstrong 1948; Lawrence 1977, 1982; Lea 1922a; D. K. Young 1978, 1985a]

**104. Aderidae** (Euglenidae; Fig. 35.57I). ADULT: ANT 11(FIL/FLAB), FCOX PROJ(CONC), FCAV OPEN(OPEN), MCOX NARR(OPEN), 5-5-4, ABD 4(0)A/5(2), 1.1–7 (1.3–3.5) mm. LARVA: HEAD PRO (PRO), STEM 0, ANT 3, FSUT 0, LABR FR, MOLA +/0R, VMP RET, MALA, MP 3, LP 2, HSC +/0R, HRD +/0R, VER 0, LEGS 5, TS 2, UROG +/0R, SPIR AN.

Elongate, convex to somewhat flattened beetles, usually resembling smaller Anthicidae in having a narrow pronotum without lateral carinae, securiform maxillary palps, and the head abruptly constricted behind the eyes; they differ from anthicids, however, in having larger, more coarsely faceted eyes, internally open fore coxae, the first 2 ventrites strongly connate or solidly fused, the antepenultimate tarsal segment lobed, and the penultimate one reduced. Many species have bicoloured elytra, and the vestiture consists of erect and/or decumbent hairs, the latter sometimes forming a pattern. In males of some species, the hind femora bear setose secretory organs. Larvae almost always narrowly elongate, parallel sided, somewhat flattened and lightly sclerotised, except for tips of urogomphi. Mandible almost always with hyaline lobe at base of mola, median endocarina on head and armature on S9 absent. Adult Aderidae are normally collected on foliage or in Malaise or flight-intercept traps, while larvae have been collected in rotten wood, under bark or in leaf litter. The Australian fauna includes *Pseudananca ruficollis*, *Syzeton*, *Syzetoninus*, *Syzetonellus* and many species described in *Xylophilus* (= *Aderus*) but belonging to several other genera. *Megaxenus* from North Qld and Melanesia (Lawrence *et al.* 1990) differs from other aderids in its large size (usually more than 4 mm long), lack of a mandibular mola in both adult and larva, lack of larval urogomphi, and termitophilous habits. [Báguena Corella 1948; Lea 1917a, b; Watt 1987]

**105. Scraptiidae** (Fig. 35.57J). ADULT: ANT 11(FIL/FLABr), FCOX PROJ(CONC), FCAV OPEN (CLOS), MCOX CONT(OPEN), 5-5-4, ABD 5/6(0), 1.3–6 mm. LARVA: HEAD PRO(PRO), STEM 0, ANT 3, FSUT +, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD 0, VER 0, LEGS 5, TS 2, UROG 0, SPIR AN.

Oblong to narrowly elongate, parallel-sided to fusiform, soft-bodied and uniformly pubescent beetles with relatively long legs and antennae. Head strongly deflexed and abruptly constricted behind eyes forming a narrow neck; frontoclypeal suture distinct; eyes coarsely

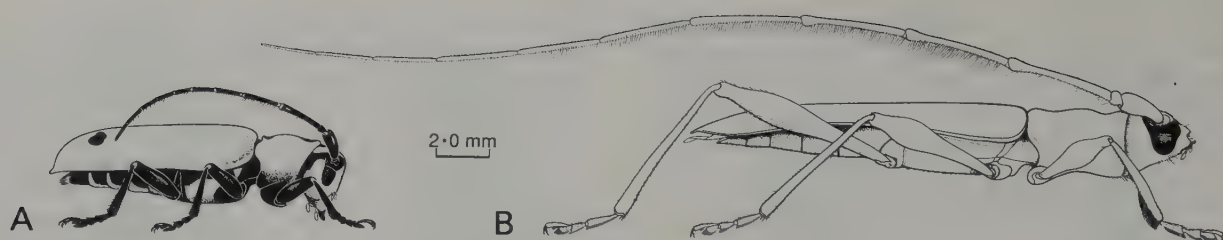


Fig. 35.58 Cerambycidae: A, *Zygrita diva*, Lamiinae; B, *Epithora dorsalis*, Cerambycinae.

[F. Nanninga]

faceted and deeply emarginate; apical segment of maxillary palp securiform; lateral pronotal carinae complete or incomplete anteriorly; tibial spurs well developed and pubescent; penultimate tarsal segment lobed beneath. Larvae elongate, parallel sided, somewhat flattened and lightly sclerotised, with oblong, setose, deciduous process (often broken off) at apex of T9. Head without median endocarina; antennal sensorium dome-like; ligula moderately long. Adult scaptiids are usually collected on flowers and foliage, and the larvae have been found under bark and in rotten wood and leaf litter. Australian species all belong to SCAPTIIINAE. *Xylophilostenus octophyllus* is unusual in having the last 8 antennal segments bearing long, flabellate processes. All other described species have been placed in the world-wide genus *Scaptia*, but several undescribed genera have been seen in collections. [Franciscolo 1972; Lawrence 1987b; Watt 1987]

#### Superfamily CHRYSOMELOIDEA (Phytophaga)

Chrysomeloids are similar to curculionoids in having pseudotetramerous tarsi, a reduced cucujoid type of aedeagus, and similar male internal reproductive organs (Kasap and Crowson 1977; Mann and Crowson 1983) in the adult and in lacking a distinct mandibular mola and gular area in the larva; they differ from weevils, however, in having well-developed mouth-parts but no rostrum or distinct antennal club in the adult and lacking a hypopharyngeal bracon in the larva. Although only two families are recognised in the present work, several subgroups of both Cerambycidae and Chrysomelidae are sometimes given family rank. Crowson (1981) recognised the family Megalopodidae (including Zeugophorinae), which is further elaborated upon by Kuschel and May (1990). Švácha and Danilevsky (1987) argued for the recognition of Vesperidae, Anoplodermatidae, Oxypeltidae and Disteniidae, all of which lack a secondary gular region considered to be an autapomorphy of the Cerambycidae proper. Chen (1985) recognised six chrysomeloid families: Megalopodidae (including Orsodacninae and Zeugophorinae), Cerambycidae, Crioceridae, Chrysomelidae, Eumolpidae and Hispidae. Ideas on relationships among chrysomelid subfamilies vary considerably from author to author. Bruchidae are usually placed in a separate family, but Mann and Crowson (1981) summarised evidence for their close relationship to Sagraeinae. Although the subfamilies Cryptocephalinae (= Camptosomata), Galerucinae (including Alticinae) and Hispinae (including Cassidinae) are generally recognised mono-

phyletic taxa, the positions of Eumolpinae, Hispinae and several smaller groups (e.g. Synetinae and Orsodacninae) differ in classifications offered by Monrós (1959a), Medvedev (1971) and Mann and Crowson (1981).

**106. Cerambycidae** (longicorn beetles, long-horned beetles; Figs 35.16H, BB, DD, 58A, B, 60A; Plates 4, G, J, K, R, 6, B, J, M, O). ADULT: ANT 11 (FIL/MON/PECT/FLAB), FCOX TRANS-PROJ(EXP-CONC), FCAV OPEN-CLOS (OPEN-CLOS), MCOX NARR-MWIDE (OPEN-CLOS), 5-5-5R/P4-4-4, ABD 5(0), 2.5-80 (8-50) MM. LARVA: HEAD PRO(RET), STEM 0-3, ANT 2/3, FSUT 0/+, LABR FR, MOLA 0, VMP PRO, MALA, MP 3, LP 2, HSC 0, HRD +, VER 0, LEGS 0/2-5, TS 0, UROG 0/+R, SPIR AN/ABR/AM.

Elongate, subcylindrical to somewhat flattened beetles, usually pubescent; antennae almost always more than two-thirds body length and inserted on prominences, so that they can be directed backwards over the body. Eyes usually emarginate, often deeply so; lateral pronotal carinae absent, except in Parandrinae and Prioninae, often with lateral tubercles or spines on prothorax; mesonotum usually with stridulatory file; tibial spurs present on all legs; tarsal claws simple. Larvae (Figs 35.16H, BB, DD 60A) elongate, subcylindrical to slightly flattened, lightly sclerotised and subglabrous or clothed with fine setae or patches of spinules. Head retracted into prothorax and excavated posteriorly, forming a recess housing a retractor muscle; antennae short; mandibles large and stout; prothorax usually more or less enlarged; legs small and widely separated and may be vestigial or absent; first 6 or 7 abdominal segments may bear fleshy ampullae which aid locomotion within wood; urogomphi, if present, minute.

Adult cerambycids are active fliers and may be diurnal or nocturnal; many feed on flowers, foliage or bark, and some are attracted to sugar baits. Larvae are phytophagous and usually feed internally on bark, phloem, sapwood or heartwood of a variety of trees and shrubs. Some species attack herbs, others are root feeders or gall formers, and a few may feed on seeds or cones.

#### Keys to the Subfamilies of Cerambycidae Known in Australia

##### ADULTS

1. Tarsal segment 4 easily visible, not concealed by lobe on segment 3; lateral pronotal carinae complete and simple; antennae short, rarely extending beyond



- posterior edge of prothorax ..... PARANDRINAE (*Parandra*)
- Tarsal segment 4 minute, concealed at base of setose lobe on segment 3; lateral pronotal carinae almost always absent, incomplete or bearing teeth or spines; antennae longer, extending at least to anterior third of elytra ..... 2
- 2(1). Lateral pronotal carinae present, sometimes incomplete and usually bearing teeth or spines; fore coxae strongly transverse with broadly exposed trochantins ..... PRIONINAE
- Lateral pronotal carinae absent; fore coxae usually less transverse, with concealed or only slightly exposed trochantins ..... 3
- 3(2). Fore tibia with internal and mid tibia with external oblique groove densely lined with setae; apical segment of maxillary palp fusiform, narrowed apically; head almost always strongly deflexed and hypognathous ..... LAMIINAE
- Fore and mid tibiae without oblique groove; apical segment of maxillary palp slightly expanded and truncate at apex; head prognathous or only slightly deflexed ..... 4
- 4(3). Antennal segment 2 more than half as long as 1 and more than a third as long as 3; antennae relatively short, not extending to middle of elytra; fore coxae strongly transverse with broadly exposed trochantins ..... ASEMINAE (*Arhopalus*)
- Antennal segment 2 less than a third as long as 1 and less than a fourth as long as 3; antennae usually longer, extending beyond middle of elytra; fore coxae usually more conical, with trochantins not or only slightly exposed ..... CERAMBYCINAE

## LARVAE

1. Legs absent or vestigial and mandible with oblique cutting edge; head distinctly oblong with sides parallel or converging posteriorly; cardines, maxillary articulating areas and submentum fused into single piece ..... LAMIINAE
- Legs usually present and well developed, or if absent or vestigial, then mandible with gouge-like cutting edge; head transverse or subquadrate with sides diverging posteriorly; cardines, maxillary articulating areas and submentum distinct ..... 2
- 2(1). Occipital foramen not divided into 2 parts (tentorial bridge internal); maxillary palpifer indistinct, not protruding laterally; ventral mouth-parts broadly attached to hypostoma; anterior edge of frons with more than 16 setae ..... ASEMINAE (*Arhopalus*)
- Occipital foramen divided into 2 parts by tentorial bridge, which is on same plane as hypostoma; maxillary palpifer distinct and laterally protruding; ventral mouth-parts narrowly attached to hypostoma; anterior edge of frons with fewer than 16 setae (usually with 4 or 6) ..... 3
- 3(2). Mandible with gouge-like cutting edge; maxillary mala broad and flat, with inner edge glabrous or almost so; clypeus narrower, not extending laterally almost to mandibular articulations; anterior edge of frons with 4 setae only ..... CERAMBYCINAE
- Mandible with oblique cutting edge; maxillary mala

slender, subcylindrical and densely setose on inner edge; clypeus broader, extending laterally almost to mandibular articulations; anterior edge of frons with 6 or more setae ..... 4

- 4(3). Posterior portion of protergum coarsely asperate; anterior edge of frons with more than 6 setae, with lower boundary not projecting over clypeus and without teeth or carina; mandible with finely striate, subapical pseudomola .... PARANDRINAE (*Parandra*)
- Posterior portion of protergum glabrous or finely pubescent, not asperate; anterior edge of frons with 6 setae, with lower boundary projecting over clypeus and with upper boundary usually carinate or dentate; mandible without striate pseudomola ..... PRIONINAE

The PRIONINAE include a number of large, dark brown species with serrate lateral pronotal carinae, such as *Paroplitus australis*, which tunnels through old *Banksia* trees, the widespread *Eurynassa australis*, and *Cnemoplites*, larvae of which (called witchety grubs) were consumed by Aborigines. Two unusual species are *Rhipidocerus australasiae* (Plate 4, G), which is light green with flabellate antennae in the male, and *Phaolus metallicus*, which is metallic blue or green. *Parandra* (PARANDRINAE) is unusual in lacking the pseudotetramerous tarsi characteristic of other Chrysomeloidea. A single species of ASEMINAE, *Arhopalus syriacus*, was introduced into N.S.W., where it attacks *Pinus*; but the Lepturinae, which are common in the Northern Hemisphere, do not occur in Australia.

The CERAMBYCINAE are the largest and most diverse group, containing a number of tribes and about 150 genera. Perhaps the best known species is *Phoracantha semipunctata*, a widely distributed eucalypt borer, which has been accidentally introduced into New Zealand, South Africa, South America, southern Europe, the Middle East, and more recently North America, where it is a serious pest of planted *Eucalyptus* (Carne and Taylor 1978; Scriven *et al.* 1986). The larva of *Bardistus cibarius*, called the bardee, was another source of food for Aborigines. *Hylotrupes bajulus*, the European house borer, has been accidentally introduced into Australia on several occasions, but in each case it was prevented from becoming established (Howick and Carr 1971). *Hesthesis* (Plate 6, J, M, O) have shortened elytra, frequent flowers, and are striking mimics of wasps both in colour and behaviour; *Macrones* resembles narrow-waisted sphecids wasps; and *Eroschema* (Plate 6, B) belongs to a lycid mimicry complex. Other notable cerambycines include *Uracanthus triangularis* (Plate 4, R), which attacks various shrubs, *U. cryptophagus*, a pest of cultivated *Citrus*, and *Diotimana undulata*, which attacks *Araucaria cunninghamii* in N.S.W. and Qld and also occurs on Norfolk I., where its host is *A. heterophylla*.

Among the LAMIINAE, the dark-coloured, flightless *Microtragus* and *Athemistus* closely resemble amycetere weevils. *Batocera wallacei* is the largest Australian beetle; *B. boisduvali* and the silvery grey *Rosenbergia megacephala* both attack fig trees in Qld. Other common lamiines include *Ancita*, which tunnels in sapwood of

*Acacia* branches, and *Platyomopsis*, *Rhytiphora* and *Penthea* (Plate 4, J, K), many of which are also *Acacia* feeders. [Duffy 1963; Froggatt 1923, 1927; McKeown 1947; G. Williams 1985]

**107. Chrysomelidae** (incl. Bruchidae, Megalopodidae; leaf beetles and seed weevils; Figs 35.59A–L, 60B–G; Plates 4, Q, 5, C, F). ADULT: ANT 9–11(FIL/MON/SERR/ PECT/INCR/3–6R), FCOX TRANS/GLOB/PROJ (EXP–CONC), FCAV OPEN–CLOS(CLOS), MCOX CONT–VWIDE(OPEN–CLOS), P4-4-4/4-4-4, ABD 5/6 (0–2), 1.2–32 (1.8–16) mm. LARVA: HEAD PRO

(PRO/RET) R/HYPO, STEM 0–6, ANT 1–3, FSUT 0/+, LABR FR/FU, MOLA 0, VMP RET/PRO, MALA, MP 1–4, LP 0R/1/2, HSC 0, HRD 0/+, VER 0, LEGS 0–3R/4/5, TS 0/1, UROG 0/+R, SPIR AN/AB/AM/CR/REDR.

Beetles with extremely varied body form, but often subglabrous and brightly coloured. Antennae variable but usually filiform, very rarely enlarged apically to form club, never inserted on prominences, usually shorter than in Cerambycidae and not extending beyond the middle of body. Head often with grooves or prominences; labrum visible; maxillae and labium well developed with flexible

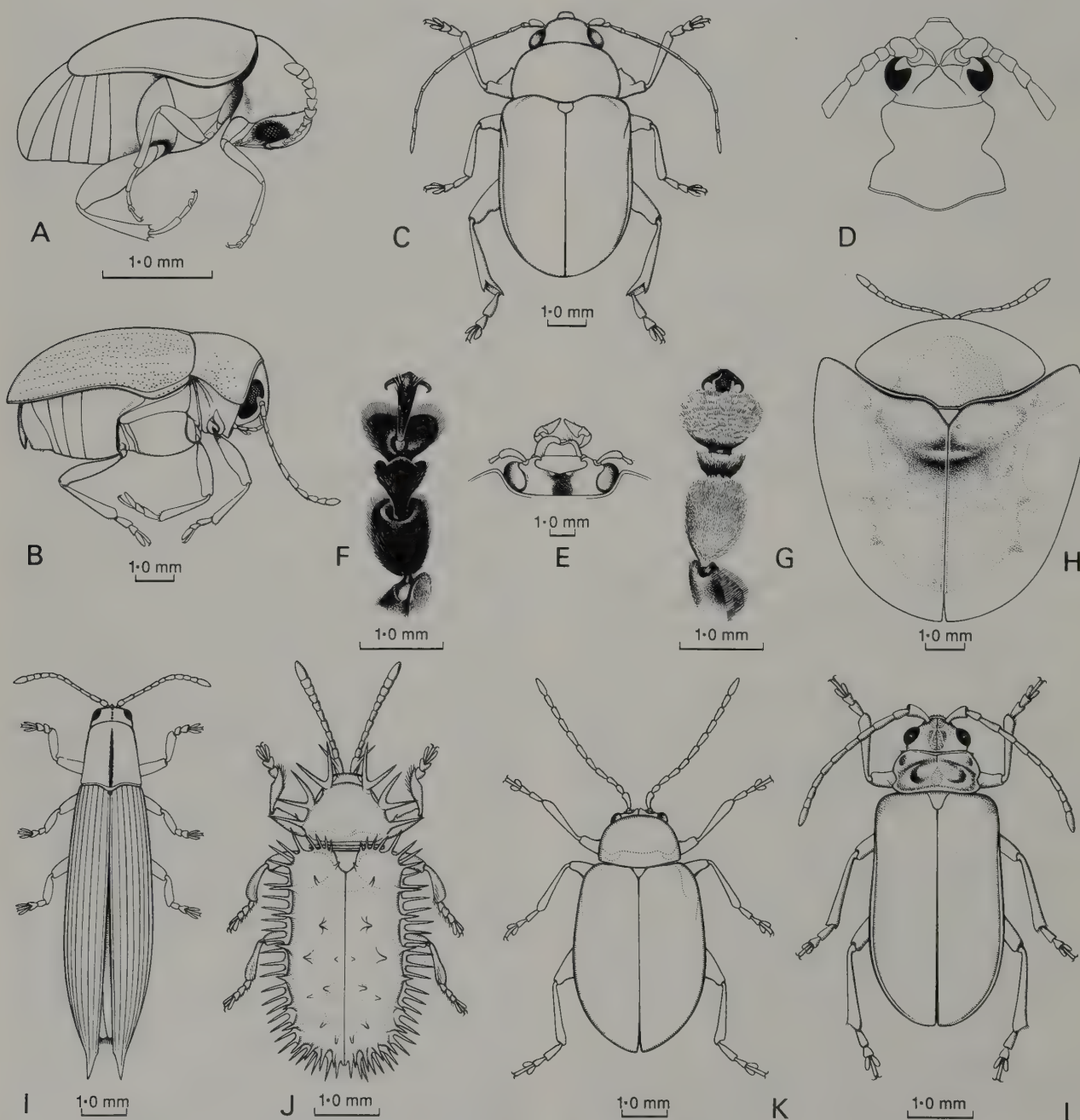


Fig. 35.59 Chrysomelidae: A, *Bruchidius lyndhurstensis*, Bruchinae; B, *Cryptocephalus haematodes*, Cryptocephalinae; C, *Edusella abdominalis*, Eumolpinae; D, *Stethopachys formosa*, Criocerinae, head and prothorax; E–G, *Sterromela trimaculata*, Chrysomelinae: E, head; F, tarsus, dorsal; G, tarsus, ventral; H–J, Hispinae: H, *Meroscalcis selecta*, Cassidini; I, *Eurispa howitti*, Hispini; J, *Hispellinus multispinosus*, Hispini; K, *Altica pagana*, Galerucinae–Alticini; L, *Poneridia australis*, Galerucinae–Galerucini.

[F. Nanninga]



palps; head may be rostrate, but rostrum not longer than wide; lateral pronotal carinae often complete but may be incomplete or absent; distinct tibial spurs not common (except in jumping Alticini); first 3 tarsal segments with lobes beneath them which are covered with spatulate or bifid, adhesive setae; 4th tarsal segment either minute and concealed at base of preceding segment (pseudotetramerous), or fused with terminal segment; tarsal claws sometimes cleft or appendiculate; basal ventrites never solidly fused as in most weevils. Larvae (Figs 35.60B–G) also highly variable, but usually lightly sclerotised, except for head and sometimes numerous small plates or protuberances, and usually with well-developed legs. Head often hypognathous with median endocarina; mandibles usually with 3 or more apical teeth; labrum free except in Cryptoccephalinae; rarely with urogomphi on T9. As far as is known, all Chrysomelidae are phytophagous, the adults feeding externally and the larvae externally or internally on a wide variety of higher plant tissues comprising roots, foliage, herbaceous stems, growing tips, leaves, flowers, pollen, fruits and seeds. Except for larvae of Cryptoccephalini, which specialise on dead leaves, most chrysomelids feed on living tissue, and few, if any, occur in wood. The Australian species may be placed in 12 subfamilies, three of which are defined more broadly than in Britton (1970).

*Keys to the Subfamilies of Chrysomelidae Known in Australia*

ADULTS

1. Head usually strongly hypognathous or opisthognathous with frons sloping posteriorly; if head less strongly declined, elytra lined with short spines or teeth and last 2 antennal segments enlarged and club-like; if head projecting forward and apparently prognathous (*Aproidea*), mouthparts projecting ventrally and mandibles moving in vertical plane; eyes never emarginate; antennal sockets usually subcontiguous, occasionally separated by slightly more than the diameter of one of them; tarsi 4-segmented (without minute penultimate segment) and with bifid adhesive setae on segments 1–3 ..... HISPINAE  
Head usually prognathous with frons sloping anteriorly; if head hypognathous, antennal sockets separated by more than twice the diameter of one of them; eyes usually emarginate and elytra not lined with teeth or spines; tarsi 5-segmented, with minute penultimate segment more or less concealed at base of segment 3 (pseudotetramerous) and with bifid setae absent or present on segment 3 only ..... 2
- 2(1). Head strongly deflexed, somewhat rostrate (Fig. 35.59A); eyes deeply emarginate or shallowly emarginate and approximate (separated by less than half the width of one as seen from above); head constricted behind the eyes to form a distinct neck; prothorax strongly narrowed from base to apex, usually with incomplete lateral carinae (at least slightly indicated at base); procoxae projecting below prosternum and contiguous; elytra striate, with rounded apices which expose all or most of pygidium; hind femora greatly inflated, with 1 or more teeth or serrations on inner edge; hind tibiae carinate with a fixed apical spine; tarsal claws toothed ..... BRUCHINAE  
Head, if strongly deflexed, not rostrate, without neck, and deeply inserted into prothorax; prothorax not narrowed from base to apex and usually without or with complete lateral carinae; if hind femora inflated, teeth or serrations usually absent and tarsal claws often simple; hind tibiae never carinate with fixed apical spine ..... 3
- 3(2). Head between antennal insertions with paired, subtriangular elevations bounded by deep grooves which form an X or H, depending upon whether apices of triangles meet at midline; pronotum much narrower than bases of elytra, without lateral carinae; head somewhat rostrate, with genae and frontoclypeus extending well in front of antennal insertions; femora more or less inflated, those of hind legs sometimes with a tooth or angular prominence on inner edge ..... 4  
If subtriangular elevations present, they are indistinct and not bounded by deep grooves, or they are located behind antennal insertions and the pronotum has distinct lateral carinae; without other characters in combination ..... 5
- 4(3). Fore coxae globular to transverse, not or only slightly projecting, well separated by complete prosternal process and usually with exposed trochantins; ventrite 1 as long as or longer than remaining ventrites taken together; length more than 8 mm ..... SAGRINAE  
Fore coxae conical and projecting, contiguous and without exposed trochantins; ventrite 1 not as long as remaining ventrites taken together; length less than 8 mm ..... CRIOCERINAE
- 5(3). Antennal sockets separated by less than 2.5 times the diameter of one of them ..... 6  
Antennal sockets separated by more than 2.5 times the diameter of one of them ..... 7
- 6(5). Lateral pronotal carinae absent; pronotum much narrower than combined elytral bases; tarsal claws simple; ventrite 1 longer than remaining ventrites combined; ventral surfaces clothed with silvery pubescence ..... DONACIINAE  
Lateral pronotal carinae present (if indistinct, tarsal claws appendiculate); ventrite 1 not as long as remaining ventrites combined; ventral surfaces not clothed with silvery pubescence ..... GALERUCINAE
- 7(5). Fore coxae conical and projecting well below prosternum; base of pronotum much narrower than combined elytral bases; lateral pronotal carinae absent or occasionally very fine; mesonotum with stridulatory file ..... MEGALOPODINAE  
Fore coxae globular or transverse, not projecting; pronotum usually as wide or nearly as wide as combined elytral bases; lateral pronotal carinae almost always well developed and complete; stridulatory file usually absent ..... 8
- 8(7). Clypeus truncate anteriorly, with a more or less membranous anteclypeus visible for its entire width and on same level as sclerotised postclypeus; head prognathous or slightly declined; fore coxae more or less transverse with exposed

- trochantins ..... CHRYSOMELINAE
- Clypeus with membranous anteclypeus absent, concealed or visible only mesally and postclypeus broadly emarginate apically with the anterior angles produced on each side; head usually strongly declined or hypognathous; fore coxae usually globular with concealed trochantins ..... 9
- 9(8). Base of pronotum at least slightly and often much narrower than combined elytral bases; pygidium usually concealed beneath elytra, or if partly exposed then provided with median groove; head usually slightly to moderately declined and not deeply inserted into prothorax (if hypognathous and deeply inserted, tarsal claws appendiculate); ventrite 5 in ♀ without deep fovea ... EUMOLPINAE
- Base of pronotum as broad as combined elytral bases; pygidium almost always partly and often completely exposed, without median groove; head almost always strongly hypognathous and deeply inserted into prothorax; tarsal claws rarely appendiculate; ventrite 5 in ♀ with distinct, usually deep, semicircular impression ..... CRYPTOCEPHALINAE
- ### LARVAE
1. Body C-shaped; head elongate and deeply retracted into prothorax; mandibles unidentate; legs usually reduced ..... 2
- If body C-shaped, head not elongate and retracted; mandibles rarely unidentate ..... 3
- 2(1). Legs well developed, 5-segmented; labial palps 2-segmented; tracheal system without air sacs; not in seeds ..... SAGRINAE
- Legs with 4 segments or fewer; labial palps absent; tracheal system with air-sacs; in seeds ..... BRUCHINAE
- 3(1). Abdominal spiracles 1 to 7 vestigial, those on segment 8 displaced dorsally and forming curved, spine-like processes (Fig. 35.18H). Feeding on water lilies in northern Australia ..... DONACIINAE
- Abdominal spiracles 1 to 7 well developed, 8 not forming spine-like processes ..... 4
- 4(3). Legs minute or absent; body straight, flattened and parallel sided or gradually tapering posteriorly ... 5
- Legs well developed ..... 6
- 5(4). Head transverse, protracted, broadly and shallowly emarginate posteriorly; maxillary palps 3-segmented and well developed ..... MEGALOPODINAE
- Head elongate, strongly retracted and deeply emarginate posteriorly; maxillary palps at most 2-segmented, sometimes highly reduced; labial palps well separated ..... HISPINAE (pt)
- 6(4). Head with several stemmata on each side; labial palps 1-segmented; body never C-shaped, although sometimes dorsally humped ..... 7
- If more than 1 stemma on each side, labial palps 2-segmented ..... 10
- 7(6). Maxillary palps 3-segmented; median endocarina absent; spiracles on segment 8 placed similarly to those on segment 7; abdomen dorsally humped; T9 simple ..... CRIOCERINAE
- Maxillary palps 2-segmented; median endocarina present (sometimes coincident with epicranial stem); spiracles on segment 8 displaced dorsally or posteriorly or T9 with long, narrow process; abdomen not dorsally humped ..... 8
- 8(7). Head prognathous; body somewhat flattened; segment 8 terminal, bearing a pair of posteriorly projecting appendages; spiracles more or less posteriorly directed, rarely located on appendages ..... HISPINAE (pt)
- Head hypognathous; body not flattened and parallel sided; segment 9 or 10 terminal; 8th spiracles not posteriorly directed ..... 9
- 9(8). Segment 9 terminal, bearing a long, narrow, posteriorly projecting process; segment 10 ventral; 8th spiracles not displaced; antennae 1-segmented; body elongate, tapering posteriorly ..... HISPINAE (*Aproidea*)
- Segment 10 terminal; segment 9 small and simple; segment 8 bearing a pair of long, narrow, anterodorsally projecting processes to which cast skins and other debris may be attached; 8th spiracles displaced dorsally; body ovate with thorax and first 8 abdominal segments bearing laterally projecting, narrow processes .... HISPINAE (Cassidini)
- 10(6). Stemmata on each side 0 or 1; antennae 2-segmented ..... 11
- With more than 1 stemma on each side; antennae almost always 3-segmented ..... 12
- 11(10). Labial palps 1-segmented; endocarina shorter, either coincident with epicranial stem or not extending far in front of it; body always lightly sclerotised and strongly curved ventrally, without sclerotised plates or protuberances; abdominal sterna usually forming projecting lobes which are densely clothed with stiff setae ..... EUMOLPINAE
- Labial palps 2-segmented; endocarina extending to clypeus; body often with sclerotised plates or protuberances, sometimes restricted to T9; abdominal sterna without setose projections .... GALERUCINAE
- 12(10). Body strongly curved and C-shaped, enclosed in faecal case; labrum partly or completely fused to clypeus and frontoclypeal suture absent; median endocarina absent ..... CRYPTOCEPHALINAE
- Body not strongly curved and not enclosed in faecal case; labrum freely articulated and frontoclypeal suture usually present; median endocarina well developed ..... CHRYSOMELINAE

The subfamily MEGALOPODINAE is represented in Australia by three genera: the widespread *Zeugophora* (subgenus *Pedrillia* = *Austrolema*, Monrós 1959b); the endemic *Cucujopsis*, which was placed by Crowson (1946) in the Orsodacninae; and *Palophagus* (Kuschel and May 1990). Larvae are unknown for the three Australian *Zeugophora*, but exotic species of *Zeugophora* (s. str.) are known to be leaf-miners in Salicaceae (especially *Populus*), and *Pedrillia* has been associated with sandalwood (*Santalum*, Santalaceae) and spindle tree (*Euonymus*, Celastraceae) (Medvedev and Zaitzev 1978; Reid 1989). Both adults and larvae of *Palophagus* feed on the pollen of *Araucaria*. DONACIINAE are represented by two species of *Donacia* (*Cyphogaster*), which occur in North Qld and N.T. (Borowiec 1984) and are associated with water lilies (Nymphaeaceae); larvae have the 8th



spiracles located in sharp spines, which can pierce plant roots to obtain air (Varley 1939).

The SAGRINAE has its greatest diversity in Australia, being represented elsewhere only by the genus *Sagra* in Africa and Asia, *Megamerus* in Madagascar and Brazil, and *Atalasis* in Argentina (Monrós 1959a). *Sagra papuana* (Plate 4, Q) occurs in North Qld; its habits are probably similar to its Asian congeners, the larvae of which feed in herbaceous stems of various plants, including wild yams (Dioscoreaceae). Among the 10 endemic genera are *Carpophagus*, whose members look like giant seed weevils (Bruchinae), *Polyoptilus*, containing cerambycid-like forms, and *Megamerus*, including our largest species (over 30 mm in length). Larvae of *Mecynoderes coxalgica* were found in cocoons in soil at the base of a *Lomandra* (Xanthorrhoeaceae), and 1st instars of an unknown sagrine from W.A. were found in a multi-chambered mud case attached to a shrub. Sagrines are noted for having enlarged hind femora bearing teeth or spines; unlike flea beetles (Alticini), however, they cannot jump. BRUCHINAE also have enlarged and spinose hind femora, but they are smaller, more compact beetles with projecting fore coxae, a declivous head, and an exposed pygidium. Unlike sagrines, they are specialised seed feeders as larvae. The Australian fauna is not rich, and most endemic species belong to *Bruchidius*. Introduced bruchines include *Caryedon serratus*, which feeds on stored peanuts, *Bruchus pisorum*, a cosmopolitan pest of growing beans and peas, and *Acanthoscelides obtectus* and several *Callosobruchus*, which damage stored beans. Two other *Acanthoscelides* have been introduced from Mexico to control the giant sensitive plant (p. 563). [Borowiec 1987; Maulik 1941]

The CRIOCERINAE is a relatively small group, most members of which feed externally on monocotyledonous plants. *Stethopachys formosa* has become a pest of commercial orchids; larvae are covered in slime and pupation occurs in a cocoon composed of foam-like pellets. The introduced *Lema trilineata* is a pest of Cape gooseberry and other solanaceous plants (Franzmann 1978).

The subfamily HISPINAE is used here in the broad sense suggested by Crowson (1955) and Chen (1985), and further breakdown into two groups corresponding to the old Cassidinae and Hispinae is not justified, since several taxa, including *Aproidea* and *Notasacantha*, are intermediate in both larval and adult features. Typical cassidines or tortoise beetles are characterised by their broadly ovate shape and by having the elytra and prothorax broadly explanate, the latter concealing the head from above. A common Australian genus is *Aspidomorpha*, the species of which have a strong preference for *Ipomoea* (Convolvulaceae) (Hawkeswood 1982). *Aproidea balyi* is an unusual species which feeds externally on the leaves of *Eustrephus* (Philesiaceae) (Monteith 1970); both adults and larvae are green in colour and well camouflaged against the foliaceous background. Pupation takes place on the leaf surface, and the pupa is suspended from the leaf by the withered larval skin. Several endemic hispines mine the leaves of palms and *Pandanus* (*Promecotheca*) or grasses (*Hispellinus*); others occur in leaf bases or

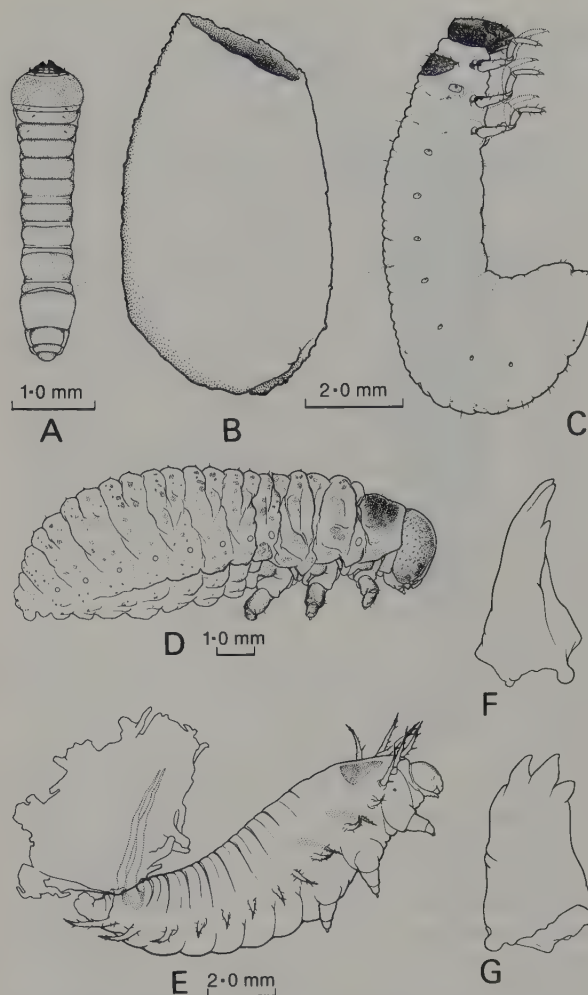


Fig. 35.60 Larvae of Chrysomeloidea: A, *Phoracantha* sp., Cerambycidae, ventral; B–G, Chrysomelidae: B, C, *Cryptocephalus parenteticus*, Cryptocephalinae, larval case and larva; D, *Lilioceris nigripes*, Criocerinae; E, *Aspidomorpha* sp., Hispinae-Cassidini, with debris attached to abdominal processes; F, G, *Altica pagana*, Galerucinae-Alticini, right mandible, external and ventral.

[A by F. Nanninga; B–G by A. Klinkenberg]

among developing leaflets of palms (*Brontispa*), sedges and grasses (*Euryspa*) or other monocotyledonous plants. The exotic leaf-miners *Octotoma scabripennis* and *Uroplata* species were introduced for the control of the dicotyledonous *Lantana* (Verbenaceae) (p. 563). [Gressitt 1957; Maulik 1931, 1932]

The CRYPTOCEPHALINAE, as understood here, includes Lamprosomatini, Chlamisini, Clytrini and Cryptocephalini, the last three of which occur in Australia. Chlamisini are represented by two native species of *Chlamisus* in Qld and a third introduced to control *Mimosa* (p. 563); Clytrini by two species in northern Australia, and Cryptocephalini by more than 20 recognised genera and 500 described species. Adults of the last group feed primarily on foliage of *Eucalyptus* and *Acacia*, and their larvae are distinctive among chrysomelids in feeding on dead leaves accumulated on the ground and in living within a close fitting portable case constructed of

faeces and debris; pupation also occurs within this case. Some of the larger Australian genera include *Cadmus*, *Cryptocephalus* and *Ditropidus*. The genus *Leasia* from W.A. has a greatly enlarged head in the male and was removed from the family by Monrós (1951); according to Crowson (1955), however, the genus has all the features of this subfamily. [Kasap and Crowson 1975; Lea 1904]

EUMOLPINAE is another large group (43 genera, ca 450 species), the larvae of which occur in soil and probably feed on roots. *Spilopyra sumptuosa* (Plate 5, C) is one of our more attractive forms. Some of the larger genera include *Edusella*, *Geloptera*, *Tomyris* and *Rhyparida*, the last of which contains economically important pests of sugar cane and other crops. [Lea 1917]

The CHRYSOMELINAE is the largest subfamily in Australia, with more than 50 described genera and in excess of 600 known species. Chrysomeline larvae, unlike those of the previous two groups, feed externally on foliage and are often armed with defence glands. The subfamily is represented by 7 of the 12 subtribes of Chrysomelini recognised by Seeno and Wilcox (1982) (the Timarchini being restricted to the Northern Hemisphere). Our most important group, the Paropsina, includes several large and common genera, such as *Paropsis*, *Paropsisterna*, *Chrysophtharta*, *Trachymela* and *Pyrgoides*. The larval defence glands, which are located on T8, secrete hydrogen cyanide (B. P. Moore 1967). Adult paropsines often have brilliant, species-specific colour patterns, but these quickly fade in dead specimens. Many paropsines are serious defoliators of eucalypts; *Chrysophtharta bimaculata* is a notorious forest insect pest in Tas., *Paropsis charybdis* has been introduced into New Zealand where it causes severe damage in gum plantations, and *Trachymela tincticollis* has become a pest in South Africa (Carne and Taylor 1978; De Little 1979; Tribe and Cillié 1985). Species of *Pyrgoides* often specialise on the flowers of *Acacia*. Other genera include *Carystea*, *Calomela*, *Stethomela*, *Chalcolampra*, *Phyllocharis* and *Lamprolina*. *Novacastria nothofagi* feeds exclusively on young leaves of *Nothofagus moorei* in northern N.S.W. (Selman and Lowman 1983). The European *Chrysolina hyperici* and *C. quadrigemina* were introduced into Australia to control St John's wort (p. 563).

GALERUCINAE is used here in the broad sense to include those forms previously included in Alticinae and known as flea beetles because of their ability to jump using the enlarged hind femora (Furth 1982; Furth *et al.* 1983). Alticine larvae are not separable from those of other galerucines, and transitional forms occur among the adults as well. The unusual endemic genus *Microdonacia* was placed in Eumolpinae by Monrós (1958) but moved to Alticinae by Jolivet (1968). Galerucines have varied habits, and larvae may feed externally on foliage but often occur in the soil and feed on roots. *Monolepta australis* attacks citrus fruit, maize and stone fruit, while adults of *Aulacophora hilaris* and *A. abdominalis* feed on foliage and flowers of cucumber, melon and pumpkin. *Rupilia* (Plate 5, F) is unusual in having shortened elytra. Flea beetles often cause 'shot-hole' damage to leaves.

*Halticorpus platycerii* specialises on staghorn and elkhorn ferns. *Agasicles hygrophila* and *Longitarsus jacobaeae* were imported from Argentina and southern Europe, respectively, for the control of noxious weeds (p. 565).

### Superfamily CURCULIONOIDEA (Rhynchophora)

This group comprises the weevils, adults of which are characterised by the elongation of the anterior part of the head to form a rostrum and the accompanying mouth-part modifications (e.g. fusion of labrum, reduction of mandibles, fusion of galea and lacinia, formation of short, rigid palps). The possession of pseudotetramerous tarsi (secondarily lost in some) and a reduced cucujoid aedeagus in the adult and the absence of a gula and reduction or loss of the mandibular mola in the larva are shared with members of the Chrysomeloidea, but the mouth-part modifications of the adult and presence of a hypopharyngeal bracon in the larva distinguish weevils from chrysomeloids. Adult weevils usually have a more or less rigid body, with closed fore and mid coxal cavities, globular fore coxae with concealed trochantins, and connation of two or more ventrites in most forms; also the antennae are almost always distinctly clubbed and usually have a long scape which may fit into a groove (scrobe) at the side of the rostrum. Larval weevils are almost always legless, but minute legs occur in some Nemonychidae, many Anthribidae and Brentidae and Ithyceridae, and well-developed legs are present in the nemonychid genus *Nemonyx*. Phytophagous habits (including pollen feeding in Nemonychidae and Allocorynidae) are almost universal in the superfamily, notable exceptions being the mycophagous species of Anthribidae.

It is generally agreed that the families Ithyceridae, Brentidae and Curculionidae, as here delimited, form a monophyletic group, based mainly on the fact that the first two ventrites are solidly fused and the last three freely movable; Crowson (1955) mentioned other features, such as the absence of a scutellary striole on the elytra. Brentidae is used here in the broad sense following Morimoto (1962, 1976) and Sanborne (1981), but Apioninae and Antliarrhininae are often given family rank. Likewise, certain groups of Curculionidae (e.g. Rhynchophorinae, Scolytinae, Platypodinae) are treated as families by various authors, including Morimoto (1962) and Wood (1978, 1986). The retraction of the larval head capsule might be used to unite Oxycorynidae, Allocorynidae, Aglycyderidae, Belidae and Attelabidae, but the condition varies in the last group and also occurs in some Anthribidae.

**108. Nemonychidae** (Fig. 35.61A). ADULT: ANT 11 (3), FCOX PROJ(CONC), FCAV CLOS(CLOS), MCOX NARR(CLOS), P4-4-4, ABD 5(0), 3-5.3 mm. LARVA: HEAD HYPO, STEM 2, ANT 1, FSUT 0, LABR FR, MOLA +, VMP RET, MALA, MP 3, LP 2, HSC +, HRD +, VER 0, LEGS 0, TS 0, UROG 0, SPIR AB.

Moderately elongate, slightly flattened beetles, clothed with decumbent hairs and usually scattered erect hairs. Rostrum elongate and flattened to subcylindrical; antennae straight with short scape and loose, weak club, inserted at middle or near apex of rostrum; labrum free and on



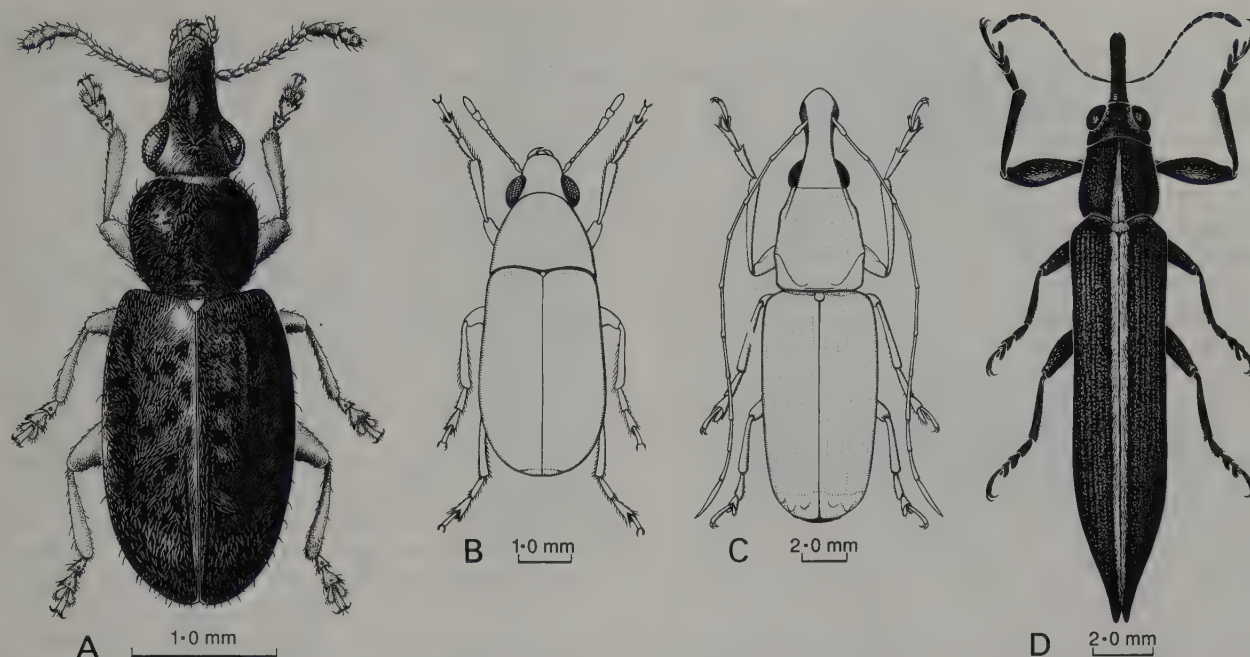


Fig. 35.61 Curculionoidea: A, Unidentified Nemomychidae; B, *Cacorhinus lateripictus*, Anthribidae; C, *Ancyclotropis waterhousei*, Anthribidae; D, *Belus suturalis*, Belidae.  
[A by A. Hastings; B–D by F. Nanninga]

same level as clypeus; mandibles acute and opposable; palps well developed and flexible; pronotum without lateral carinae; 1 or 2 stridulatory files on mesonotum; all tibiae with 1 or 2 spurs; tarsal claws toothed or bifid; ventrites freely articulated; pygidium more or less concealed by elytra. Larvae elongate, slightly to moderately curved ventrally, slightly flattened and lightly sclerotised, except for head capsule and prothoracic tergal plate, and with a pair of well-developed transverse folds on thoracic and most abdominal terga. The head is moderately deflexed; the epicranial stem is short, and there is a long median endocarina extending well in front of it. Both adult and larval nemomychids are pollen feeders, and Australian species have all been recorded from male cones of Araucariaceae (*Araucaria* and *Agathis*). Australian species all belong to undescribed genera of the subfamily RHINORHYNCHINAE, which also has representatives in Papua New Guinea, New Caledonia, New Zealand and South America. [Kuschel 1983]

**109. Anthribidae** (Figs 35.61B, C). ADULT: ANT 11(FIL/3), FCOX GLOB-PROJ(CONC), FCAV CLOS (CLOS), MCOX MWIDE(CLOS), P4-4-4, ABD 5(4), 1.5–20 mm. LARVA: HEAD HYPO/PRO(RET)<sub>R</sub>, STEM 0/1, ANT 1, FSUT +, LABR FR, MOLA 0/+, VMP RET, MALA/GLAC, MP 2/3, LP 0<sub>R</sub>/1/2, HSC +, HRD 0/+, VER 0/+, LEGS 0–3, TS 0, UROG 0, SPIR AN/AU, AB.

Moderately elongate to ovate, slightly to strongly convex beetles, usually clothed with black, brown and/or white decumbent hairs or scales forming pattern. Rostrum very short to moderately long and more or less flattened; antennae straight, very long in some males, with club which may be indistinct; labrum free and either on different plane from clypeus or separated from it by membrane; mandibles well developed and more or less acute; palps

well developed and flexible; gular sutures absent; pronotum usually with transverse, sub-basal carina joined to lateral carinae, which may be very short to complete; legs without tibial spurs; tarsi usually toothed or cleft; pygidium exposed beyond edges of elytra. Pheromone-producing setiferous sex patches are sometimes found in males on the ventrites or occasionally in other locations (B. A. Holloway 1985). Larvae short, broad, more or less C-shaped, very lightly sclerotised; antennae minute; legs highly reduced without claws, or absent. Frontoclypeal suture present; clypeus narrower than frons; mandibles robust; mala with thorn-like lacinia near middle of internal edge; most abdominal terga with 2 transverse folds. Most anthribid larvae feed in dead wood, but some are associated with the fruiting bodies of certain fungi (Ascomycetes: Pyrenomycetes) and others feed on seeds of various kinds. *Araecerus fasciculatus* is a cosmopolitan pest of coffee, cocoa beans and spices; *A. palmaris* is unusual in that the larva develops in dried fruits. [B. A. Holloway 1982]

**110. Belidae** (Fig. 35.61D; Plate 6, D). ADULT: ANT 10(FIL/INCR/4<sub>R</sub>), FCOX PROJ(CONC), FCAV CLOS (CLOS), MCOX NARR(OPEN/CLOS<sub>R</sub>), P4-4-4, ABD 5(0), 5–23 mm. LARVA: HEAD PRO(RET), STEM 3, ANT 2, FSUT +, LABR FR, MOLA 0, VMP RET, MALA, MP 3, LP 2, HSC 0, HRD 0, VER 0, LEGS 0, TS 0, UROG 0, SPIR AN.

Elongate, usually more or less parallel-sided beetles, clothed with decumbent hairs. Rostrum usually moderately long (rarely short and broad); antennae straight, lacking distinct club (rarely with weak, 4-segmented club), inserted at middle or near base of rostrum; labrum not visible; palps more or less rigid; gular sutures short and separate; pronotum without lateral carinae; tibiae usu-



ally with row of small granules along outer edge and fore tibiae often with teeth on inner edge; pygidium concealed. Larvae broad, slightly flattened, ventrally curved, lightly sclerotised and hairy, with enlarged, strongly declivous prothorax. Head elongate with indistinct median endocarina; frons sometimes with median spine; labral rods absent; mala simple and rounded; maxillary palpifer well developed; protergum with sclerotised, keeled plate on posterior half; abdominal terga with 2 indistinct transverse folds. Belid larvae are known to bore into wood, and some are relatively common in the branches and twigs of *Acacia*. Adults fly actively during the day, and species of *Rhinotia* are mimics of Lycidae. The subfamily BELINAE includes the large genus *Belus*, which extends into New Guinea, and *Rhinotia*, which also occurs in New Zealand. Australian genera of PACHYURINAE include *Pachyura* (also in New Zealand), *Agnesiotis*, *Cyrotypus* and *Leba*. [Kuschel 1959; Vanin 1976]

**111. Attelabidae** (incl. Rhynchitidae; Fig. 35.62A). ADULT: ANT 11(3), FCOX PROJ(CONC), FCAV CLOS(CLOS), MCOX CONT-NARR(CLOS), P4-4-4, ABD 5(0AR/3/4), 1.4-7 mm. LARVA: HEAD PRO (RET)/HYPO, STEM 0/1, ANT 1/2, FSUT +, LABR FR, MOLA 0, VMP RET, MALA, MP 2, LP 2, HSC 0, HRD +, VER 0, LEGS 0, TS 0, UROG 0, SPIR AB.

Oblong to slightly elongate beetles, narrowed anteriorly and subglabrous or clothed with decumbent and erect hairs. Rostrum short, flattened and apically expanded (*Euops*) or long and narrow; antennae straight and inserted dorsally or ventrally (*Car*) at base of rostrum; gular sutures fused; mandibles exodont (with outwardly projecting teeth) except in *Euops*; labrum not visible; maxillary palps well developed, but labial palps may be highly reduced; prothorax much narrower than elytral bases and without lateral carinae; tarsal claws connate at base, except in *Car*, and cleft in *Auletobius*; pygidium partly or completely exposed in *Euops*; first 3 or 4 ventrites solidly fused, except in *Car*, where they are separated by deep grooves and thus appear movable. Known larvae are relatively short and broad, strongly curved, somewhat narrowed at each end and very lightly sclerotised. Head strongly retracted in some Rhynchitinae but only slightly so in Attelabinae; labral rods present; most abdominal terga with 2 transverse folds (sometimes indistinct); some Rhynchitinae with bands of tergal asperities. Three distinct groups are represented in Australia: RHYNCHITINAE (*Auletini*, *Auletobius*), ATTELABINAE (*Attelabini*, *Euops*), and *Car*. Rhynchitinae have varied habits, some laying their eggs in terminal shoots, flower buds or fruits, and others mining leaves; the habits of Australian *Auletobius* are not known, but exotic *Auletini* breed in acorns of *Quercus* and have been associated with *Cistus* and *Tamarix*. Attelabinae are leaf rollers, the female laying eggs in cut portions of leaves, which she curls forming a roll in which the larvae develop; *Euops*

in Australia forms leaf rolls on *Eucalyptus* and *Acacia*. The position of *Car* has been disputed, but Kuschel (1983) considered it to be a rhynchitine, related to the South American *Caenominurus* and the Cretaceous *Baissorhynchus*. *Car* has been associated with species of *Callitris* (Cupressaceae), but its exact habits are not known. [J. C. M. Gardner 1934; Hoffmann 1958]

**112. Brentidae** (incl. Apionidae; Figs 35.62B, C). ADULT: ANT 9-11(FIL/MON/INCR/1/3), FCOX GLOB-PROJ(CONC), FCAV CLOS(CLOS), MCOX NARR-MWIDE(CLOS), P4-4-4, ABD 4R/5(2), 1.5-40 mm. LARVA: HEAD HYPO, STEM 0, ANT 1, FSUT +, LABR FR, MOLA 0, VMP RET, MALA, MP 2, LP 1/2, HSC 0, HRD +, VER 0, LEGS 0-2, TS 0, UROG 0, SPIR AN/AB.

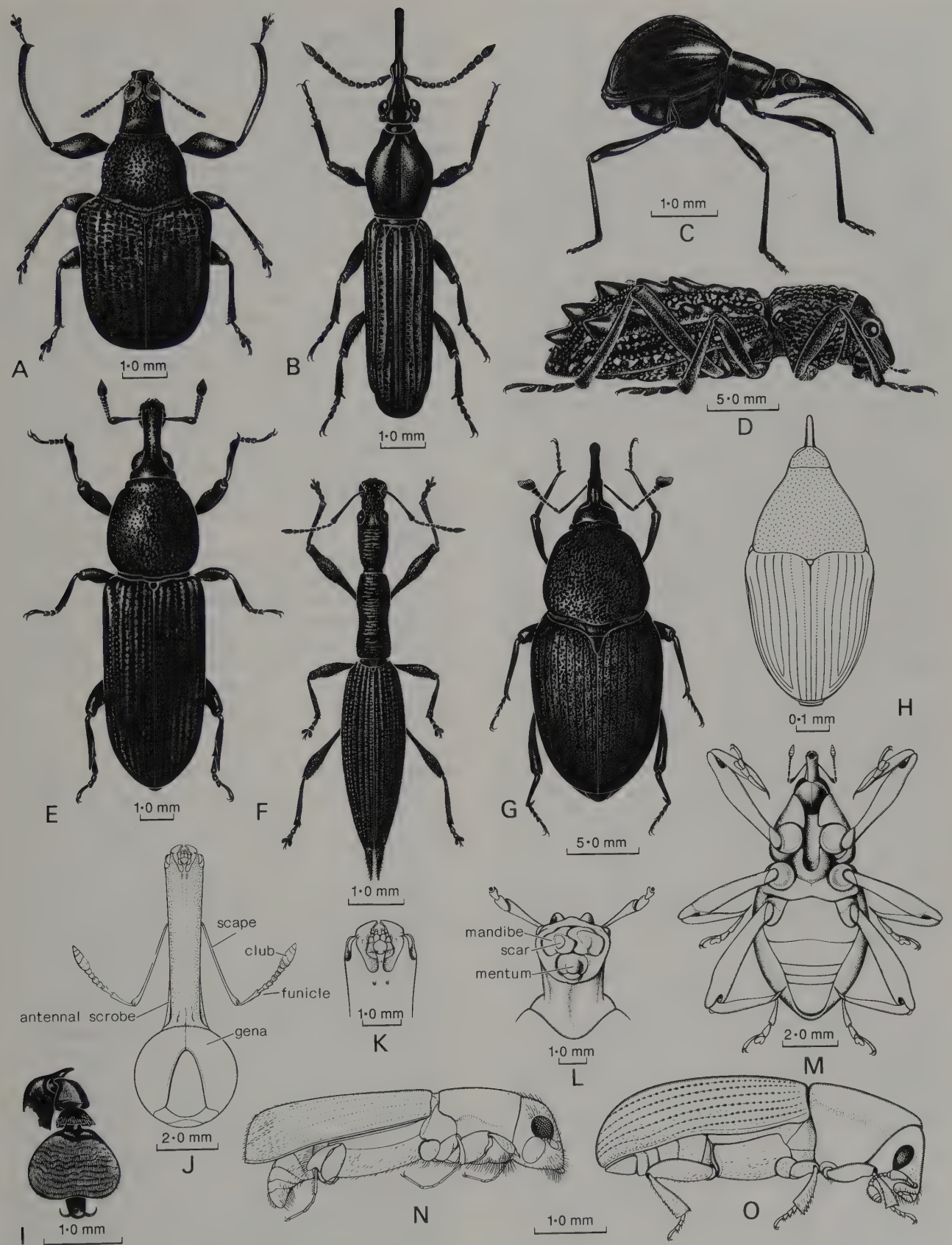
Moderately to very elongate, parallel-sided to anteriorly narrowed beetles, usually subglabrous but occasionally clothed with decumbent or erect hairs. Rostrum usually long and narrow (short and broad in some Brentinae); antennae straight with short scape, except in *Nanophyes*, where antennae are geniculate with very long scape; antennal club, when present, may be long and distinctly segmented (Eurhynchinae, Nanophyinae, some Brentinae), short, compact and indistinctly segmented (Apioninae) or unsegmented (Cyladinae); antennal insertions usually between base and middle of rostrum, but occasionally near apex; labrum not visible; maxillae and labium reduced, with rigid maxillary palps and labial palps reduced and usually concealed on inner surface of labium; gular sutures fused; prothorax without lateral carinae; pygidium concealed by elytra; first 2 ventrites solidly fused and much longer than ventrites 3-5 combined. The subfamily Brentinae includes distinctive beetles which may be very long and narrow, usually have more or less moniliform antennae, and may exhibit strong sexual dimorphism; males have a flattened and apically expanded rostrum and large mandibles and females a narrow, straight rostrum with minute mandibles. Larvae slender and subcylindrical or short and broad, moderately to strongly curved and very lightly sclerotised. Frontal arms extending to mandibular articulations; labrum with pair of sclerotised rods; mesotergum armed with paired patches of asperities in some Brentinae; abdominal terga with 2 or 4 transverse folds; legs, if present, minute and sometimes consisting of dome-like lobes only.

There are 5 subfamilies in Australia: EURHYNCHINAE (*Eurhynchus* and *Aporhina*), CYLADINAE (*Cylas*), NANOPHYINAE (*Nanophyes*), APIONINAE (*Myrmacielus*, *Apion* and relatives), and BRENTINAE, with a number of genera. *Cylas formicarius elegantulus* is an introduced pest of sweet potato in eastern Australia, while many Apioninae are known to feed on the pods of legumes. A species of *Nanophyes* was found feeding in the stems of *Ludwigia* (Onagraceae), an aquatic plant. Larvae of Brentinae are usually found in wood, and some

Fig. 35.62 Curculionoidea: A, *Euops falcata*, Attelabidae; B, *Euschizus internatus*, Brentidae-Brentinae; C, *Apion convexipenne*, Brentidae-Apioninae; D-O, Curculionidae: D, *Macramycterus boisduvali*, Amycterinae; E, *Cossonus simsoni*, Cossoninae; F, *Rhadinostomus lacordairei*, Rhadinostominae; G, *Trigonotarsus rugosus*, Rhynchophorinae; H, *Myctides imberbis*, Baridinae; I, *Diatethes morio*, Rhynchophorinae, tarsus, ventral; J, K, *Orthorhinus cylindrirostris*, Molytinae, head, ventral; L, *Leptopius* sp., Entiminae, head, ventral; M, *Paleticus subereus*, Cryptorhynchinae, ventral; N, *Platypus subgranosus*, Platypodinae; O, *Hylastes ater*, Scolytinae.

[F. Nanninga]





Calodromini utilise the galleries of scolytine and platypodine weevils. [J. C. M. Gardner 1935; Kissinger 1968; Morimoto 1976]

**113. Curculionidae** (incl. Platypodidae, Scolytidae; Figs 35.13C, 62D–O, Plates 4, I, 5, A). ADULT: ANT 7–11(1–4), FCOX PROJ(CONC), FCAV CLOS(CLOS), MCOX CONT–VWIDE(CLOS), 5-5-5R/P4-4-4, ABD 5/6R(2), 0.8–60 (1.5–40) MM. LARVA: HEAD PRO(RET) R/HYPO, STEM 0–2, ANT 1, FSUT 0/+, LABR FR, MOLA 0, VMP RET, MALA, MP 1/2, LP 1/2, HSC 0, HRD 0, VER 0, LEGS 0, TS 0, UROG 0, SPIR AN/AU/AB.

Highly variable in form, but usually moderately to strongly convex, robust, heavily sclerotised and often clothed with scales or bristles. Head always more or less produced in front of eyes to form rostrum, which is usually much longer than broad (Figs 35.62J, K); antennae always geniculate with long scape and more or less compact club; labrum absent; maxillae reduced, with short, rigid palps; gular sutures fused; penultimate tarsal segment minute and concealed at base of lobed 3rd segment, except in Platypodinae. Larvae (Fig. 35.13C) more or less C-shaped and very lightly sclerotised, with minute antennae and robust mandibles. Most groups of curculionids are phytophagous, with the larvae almost always feeding internally in plant tissue of various kinds, and the rostrum is thought to have evolved as a means of boring into plant tissue to form an egg cavity. Some weevil groups, like Cossoninae and Cryptorhynchinae, utilise rotten wood or bark, and Platypodinae and some Scolytinae feed on ambrosia fungi.

The classification of Curculionidae has improved slightly since the publication of the 1st edition (Britton 1970), but there are still many problems, and there are no workable keys to the many subfamilies and tribes. A new general scheme of classification is being proposed by G. Kuschel (in preparation), and E. C. Zimmerman's *Australian Weevils* (in press) will contain many new generic and tribal assignments. The subfamily scheme used here is from Wibmer and O'Brien (1986), which was influenced to some extent by the ideas of Kuschel. For obvious reasons, a key has not been given here, but some of the major diagnostic features of common subfamilies will be mentioned in the text.

The POLYDROSINAE and ENTIMINAE, commonly referred to as the Adelognatha, are characterised by having a relatively short, stout rostrum, a conspicuous scar (Fig. 35.62L) on the outer surface of each mandible (left by the detachment of a tooth used by the adult to escape from the pupal cell), concealed maxillae, and soil-dwelling larvae which often feed on roots. Polydrosines include the brightly coloured clown weevils (*Pantorhytes*) of Papua New Guinea, one species of which extends into North Qld, and also a number of introduced pests, such as *Otiorynchus*, *Asynonychus cervinus* (Fuller's rose weevil), *Graphognathus leucoloma* (whitefringed weevil), *Sitona discoideus*, and *Phlyctinus callosus* (garden weevil). Entiminae differ in having more elongate eyes and a rounded prothoracic lobe behind each eye. Species of *Leptopius*, called wattle pigs, are very common and some

have become pests of sugar cane and fruit trees. The fossil remains of their large pupal cases are often encountered in S.A. and W.A. (Lea 1925).

The ATERPINAE include the diamond beetle or Botany Bay weevil (*Chrysolopus spectabilis*, Plate 5, A), a spectacular green or blue species, whose larvae may destroy young *Acacia* trees. *Rhadinosomus* spp. (RHADINOSOMINAE) (Fig. 35.62F) are extremely elongate weevils, which have each elytron terminating in an acute process. The AMYCTERINAE (Fig. 35.62D) is a large subfamily of robust, ground-dwelling weevils, which have a very short rostrum, very large, chisel-like mandibles, and in some cases (*Phalidura*) a pair of forceps at the abdominal apex in the male. Amycterines are confined to Australia and feed on a variety of monocotyledonous plants, especially Poaceae and Liliaceae, the larvae living in the soil and feeding on underground stems, crowns, tubers or rhizomes (A. T. Howden 1986). Species of *Gonipteris* and *Oxyops* (GONIPTERINAE) are unusual in having an external, foliage-feeding, slug-like larva; *G. scutellatus* was accidentally introduced into New Zealand, Africa and South America, where it has become a pest of eucalypts. The DIABATHRARIINAE includes *Strongylorhinus ochraceus*, whose larvae live gregariously in large galls on eucalypts.

The subfamily RHYTIRHININAE includes species of *Aphela*, which live on beaches associated with dune vegetation, as well as two pests imported from southern South America, the vegetable weevil (*Listroderes difficilis*) and the Argentine stem weevil (*Listronotus bonariensis*). MOLYTINAE is a large group including two of our most impressive weevils, *Orthorhinus cylindrirostris*, the elephant beetle, and *Eurhamphus fasciculatus* (Plate 4, I), a large and rare species the larvae of which tunnel into the wood of hoop pine (*Araucaria cunninghamii*). Also included are *Tranes*, which have large eyes, almost meeting beneath the head, and are associated with the cones of cycads and flower stalks of *Xanthorrhoea*, and members of the Phrynixini, which feed in fern fronds and have many relatives in New Zealand. Our main representative of CLEONINAE is *Lixus mastersi*, while MAGDALIDINAE includes species of *Saccolaemus*, which have truncate elytra and an exposed, horizontal pygidium. Within the EIRRHININAE are a number of aquatic weevils, which have a ventral plastron in the adult and various respiratory adaptations in the larva. Included is *Cyrtobagous salviniae*, which was introduced from Brazil to control salvinia (Calder and Sands 1985; pp. 235, 563). RHYNCHAENINAE are very small, distinctive species with enlarged hind femora used in jumping; the larvae are leaf miners.

Members of the large subfamily CRYPTORHYNCHINAE are typically rather long-legged weevils with a long, backwardly directed rostrum, which is usually received into a channel formed between the fore coxae and often terminating in a receptacle on the mesosternum (Fig. 35.62M). *Psepholax* are unusual in having a much shorter rostrum and resembling bark beetles (Scolytinae) in general form. The genus *Melanterius* includes a large number of species which attack the seed pods of *Acacia*. *Tentegia* are unusual in that their larvae subsist on dung pellets of



wallabies and kangaroos (Macropodidae), which are placed by the adults in excavations beneath logs (Wassell 1966). Other notable examples are the mango seed weevil, *Sternochaetus mangiferae*, and *Axionicus insignis*, which breeds in the seed pods of kurrajong (*Brachychiton populneum*). The ZYGOPINAE are very long-legged tropical weevils with large, contiguous eyes. Both BARIDINAE (Fig. 35.62H) and CEUTORHYNCHINAE have a small, exposed pygidium and mesepimera which are visible from above between the pronotum and elytral humeri. COSSONINAE (Fig. 35.62E) is a large subfamily world-wide, but is primarily tropical in distribution. They are relatively small, elongate weevils, with a short rostrum, widely separated fore coxae and usually a curved spine at the tibial apex; larvae and adults may be found beneath the bark of rotten logs. There are not many named Australian species, but many remain to be described. The RHYNCHOPHORINAE are usually characterised by having an exposed pygidium and a shiny antennal club, which is pubescent at the apex only. *Trigonotarsus rugosus* (Fig. 35.62G) is a large, wood-boring species. *Rhabdoscelus obscurus* and *Cosmopolites sordidus* are pests of sugar cane and bananas, respectively, while *Sitophilus granarius*, *S. oryzae* and *S. zeamais* are important stored product pests.

The subfamilies SCOLYTINAE (Fig. 35.62O) and PLATYPODINAE (Fig. 35.62N) are often treated as separate families, mainly on the basis of the extremely short rostrum and associated differences in the tentorium and mandibular articulations (Wood 1978, 1986). Platypodines and some of the more derived scolytines also

have narrow tarsi and lack the lobed 3rd segment characteristic of most weevils. Scolytinae are usually referred to as bark beetles, because the majority of them construct galleries in the phloem layer beneath the bark of living or dead trunks, branches or twigs, and have characteristic gallery patterns resulting from the tunnelling of larvae away from the oviposition sites in the brood gallery; some species, like *Coccotrypes dactyliperda*, however, are seed feeders. Species of *Xyleborus* and some related genera and all members of the Platypodinae bore into sapwood and heartwood and feed on yeast-like ambrosia fungi (Ascomycetes: Endomycetales), which grow on the tunnel walls and are transported and cultured by the beetles; these are often called ambrosia beetles, shot-hole borers or pinhole borers. Several Northern Hemisphere scolytines have been accidentally introduced into Australia. These include *Scolytus multistriatus* which transmits Dutch elm disease; *Ips grandicollis*, which damages pine plantations (Morgan 1967); *Hylastes ater* and *Hylurgus ligniperda*. Two common platypodines are *Crossotarsus omnivorus* and *Platypus subgranosus*.

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## Strepsiptera

J. KATHIRITHAMBY

Endopterygote Neoptera with reduced mandibulate mouth-parts, extreme development of metathorax, reduced prothorax, and without differentiated trochanters in fore and mid legs. Adult males free living, with functional hind wings and small haltere-like fore wings. Females larviform, viviparous; usually parasitic, in puparium, and then with secondary progoneate genital apertures. Heteromorphosis during larval growth. 1st instar larvae free living and active, later instars parasitic.

Strepsiptera are entomophagous parasitoids which exhibit extreme sexual dimorphism. The adult male (Fig. 36.1) is free living, whereas the adult female (Fig. 36.3) is neotenic and permanently endoparasitic in the host, except in the family Mengenillidae where the female (Fig. 36.2) late larval instar (like the male) emerges from the host to pupate externally. The only other free-living stage of the order is the 1st instar larva (Fig. 36.5) which emerges viviparously from the neotenic female and seeks a new host to parasitise. The reduced mesothoracic wings,

together with the expanded hind wings in Strepsiptera, give them a superficial resemblance to Rhipiphoridae (Coleoptera); they have therefore been included by several workers as a group within the Coleoptera (Arnett 1968; Crowson 1960, 1981; Ross *et al.* 1982). Strepsiptera differ from the Coleoptera in thoracic structure, in the structure and position of their fore and hind wings, in the absence of the gula and trochanter, and in the formation of the puparium (Kathirithamby 1990a). The use of the hind wings for flight, and of the modified metathorax to

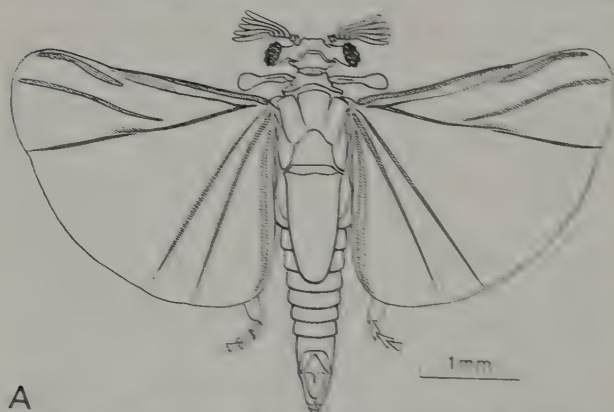


Fig. 36.1 *Coriophagus rieki*, Haliictophagidae, adult: A, dorsal; B, head, ventral.

[A by R. Ewins, B by K. Pickens]



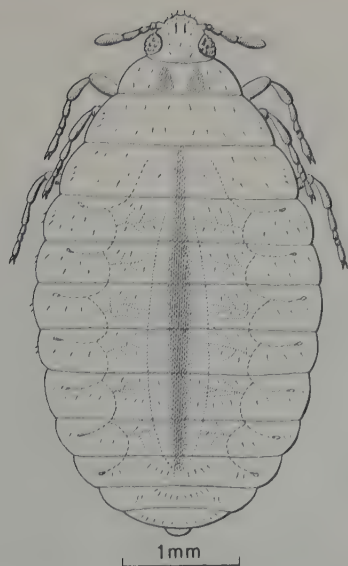


Fig. 36.2 *Eoxenos laboulbenei*, Mengenillidae, adult ♀, dorsal.  
[After Parker and Smith 1933]

accommodate the flight muscles, suggest that Strepsiptera have a sister group relationship with the Coleoptera.

Of the 532 species described from various parts of the world, only 27 are Australian (Perkins 1905; Lea 1910b; Ogloblin 1923, 1926; Kogan and Oliveira 1964; Kinzelbach 1971a; Kifune and Hirashima 1983, 1987, 1989; Drew and Allwood 1985; Kathirithamby 1989, 1990a, b). Many more species await description (as many as 160 of them from Australia).

Strepsiptera are parasitic in Thysanura, Blattodea, Mantodea, Orthoptera, Hemiptera, Diptera and Hymenoptera, but their hosts are principally among Hymenoptera and Auchenorrhyncha (Hemiptera). Parasitism by Strepsiptera is termed *stylopisation*.

Kinzelbach (1971a, b) and Kathirithamby (1989) give detailed accounts of the morphology, internal anatomy, biology and systematics of the order.

**Anatomy of Adult**

**Male** (Figs 36.1, 8, 9)

**Head.** The flabellate antennae and berry-like eyes are conspicuous features of the head (Figs 36.1, 8, 9). The antennae vary from 4–7 segments with a sensorium on the 4th or 3rd (in the Elenchidae due to fusion of the 3rd and 4th segments) segment.

The eyes are made up of 15–150 ommatidia separated by distinct strips of cuticle or setae (Figs 36.1b, 9). Mandibles are present in all the families except in the Corioxenidae, and are blade-like, conical, or knife-shaped. The maxillae vary in size (Figs 36.1b, 9), the longest being found in the family Bohartillidae.

**Thorax.** The prothorax is small, saddle-shaped and inconspicuous. The mesothorax bears the anterior pair of wings which are analogous to the halteres of Diptera. The metathorax is large and contains the principal flight muscles which are of the asynchronous type (Smith and Kathirithamby 1984). The hind wings are large with

reduced venation (Fig. 36.8). The interpretation of strepsipteran wing venation has been the subject of controversy. According to the scheme of Kinzelbach (1971a) (Fig. 36.8A), who compared the wing bases with those of various Holometabola, most of the anterior veins are part of the radial system, while the posterior portion of the fan-shaped wing contains branches of MA and Cu. A similar scheme is used by Kukalová-Peck (Chapter 6; Fig. 6.28F), who interprets the last one or two veins in the wing as anals. Crowson (1981) offered an alternative scheme based mainly on comparisons with reduced wings of beetle groups like rhipidiine Rhipiphoridae, certain Elateroidea and the cerambycid *Molorchus*. According to Crowson, the radial system is highly reduced, the median vein consists of a single apical remnant (Kinzelbach's R<sub>3</sub>), the cubitus is Kinzelbach's R<sub>4</sub>, and the remaining veins are anals.

**Legs.** The trochanter is absent in the fore and mid legs, and the hind legs have no coxa and begin with the trochanter. Mengenillidae, Mengeidae and Triozocerinae (Corioxenidae) have 5-segmented tarsi with claws, whereas in the other groups the number of tarsal segments is reduced to 4, 3 or 2 and the claws are lost; the extralimital Uniclaviniae (Corioxenidae) are exceptional in having 4-segmented tarsi and a single claw-like structure.

**Abdomen.** There are 10 abdominal segments. The 9th segment bears the copulatory organs which are simplified and there are no parameres.

**Female** (Figs 36.2, 3, 4)

The female Mengenillidae are free living with a distinct head, eyes, antennae, legs and a genital orifice, but are wingless (Fig. 36.2). The complex eyes are similar in

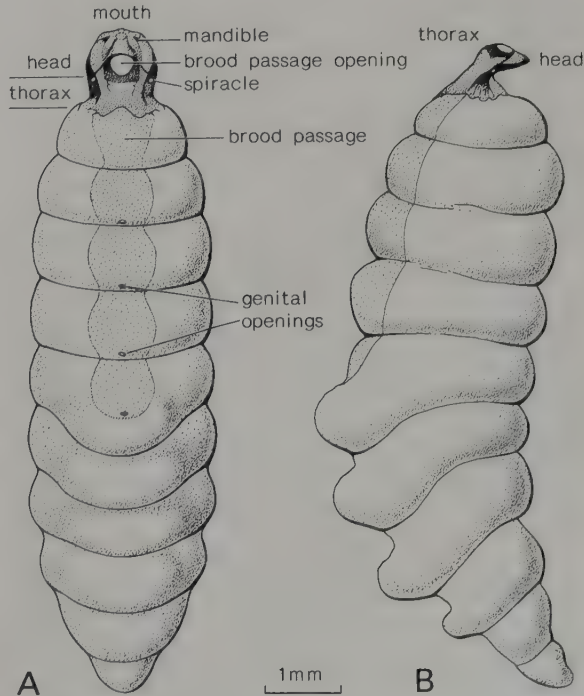


Fig. 36.3 *Coriophagus rieki*, Halictophagidae, adult ♀: A, ventral; B, lateral, dorsal surface to right.  
[R. Ewins]



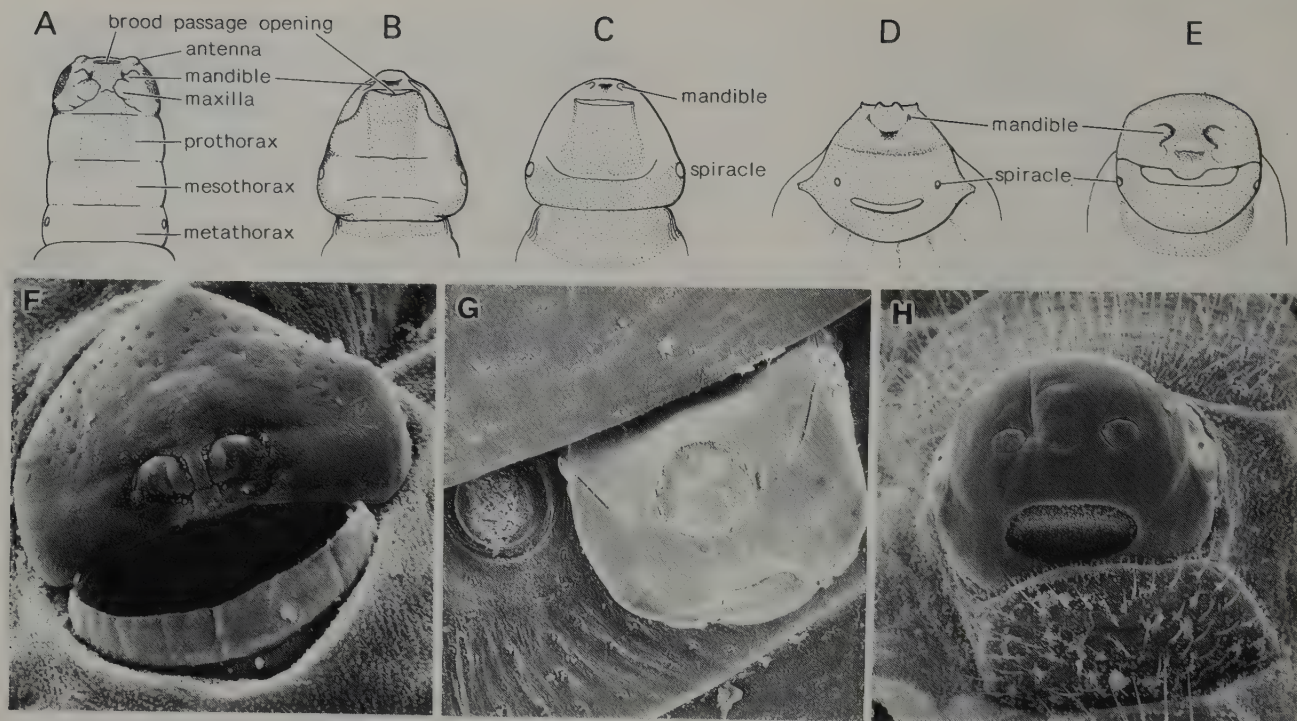


Fig. 36.4 Cephalothorax of ♀♀: A, *Corioxenos* sp., Corioxenidae; B, *Pseudoxenos* sp., Stylopidae; C, *Hylecthrus* sp., Stylopidae; D, *Stichotrema* sp., Myrmecolacidae; E, *Deinelenchus* sp., Elenchidae; F, *Elenchus varleyi*, Elenchidae; G, *Coriophagus rieki*, Halictophagidae; H, *Dipterophagus daci*, Halictophagidae.  
[A–E by R. Ewins; F–H by B. M. Luke]

structure to those in the males, but there are fewer ommatidia. The antennae are simple, with 4–5 segments.

In the Stylopidia, the females, unlike the males, become neotenic adults after extrusion of the cephalothorax at the late last larval instar. The head, pro- and mesothoracic segments tan to form the cephalothorax (Figs 36.3, 4), and the abdominal segments within the host remain soft skinned. The outer cuticle of the sexually mature female is the last larval cuticle, and through the role it plays in respiration, reproduction and food absorption, it remains an integral part of the adult female.

Kinzelbach (1971a) states that there is a partial pupal instar and the brood canal is a space formed between the last larval and pupal cuticles. The sexually mature female has functionless and rudimentary eyes, antennae, maxillae and mandibles; legs, wings and external genitalia are absent. The male fertilises the female through the brood-canal opening present in the externally visible cephalothorax or through the body wall in the brood-canal region. Nasonow's glands, on the cephalothorax, produce a pheromone which attracts males (Lauterbach 1954; Kinzelbach 1971a). The abdomen ends blindly. The openings of the genital ducts are on the 2nd–5th segments.

#### Internal Anatomy

In the adult male the oesophageal, thoracic and some or all of the abdominal ganglia form a common ganglionic mass; the remaining abdominal ganglia may coalesce to form a separate mass in the abdomen. The nervous system in the female Stylopidia is simplified.

The digestive tract is simple and ends blindly behind

the mid gut in both sexes. There are 2–3 Malpighian tubules.

The respiratory system is secondarily simplified. In male Mengenillidae it opens by 2 thoracic and 7 abdominal spiracles. Male Corioxenidae have open spiracles on the meso- and metathorax and the 1st abdominal segment and in male Halictophagidae, Elenchidae and Myrmecolacidae, the 1st and 2nd abdominal spiracles are divided and very small; in males of all other families the 1st abdominal spiracle is the largest and most efficient. In female Mengenillidae the respiratory system is similar to that of the males except that there are 2 closed spiracles in the meso- and metathorax, and the spiracles of the 8th abdominal segment are closed as in the male. In female Stylopidia the only functional spiracle is that of the 1st abdominal segment which has migrated into the cephalothorax, as in the male puparium. There is an additional closed spiracle on the thorax in some *Halictophagus* and *Coriophagus*.

The female reproductive system consists of a pair of simple tubes which break down in the 3rd larval instar, distributing the oocytes in the haemocoel.

#### Immature Stages

**First Instar Larva** (Fig. 36.5). First instar larvae are very small (0.08–0.30 mm in length) and free living. The head bears stemmata, antennae, mandibles and the labium. The dorsal thoracic and abdominal tergites are very smooth, whereas the ventral sternites are highly serrated (Figs 36.5C, D), presumably to enable the larvae to cling to the host. The legs have a trochanter (Schneiderit



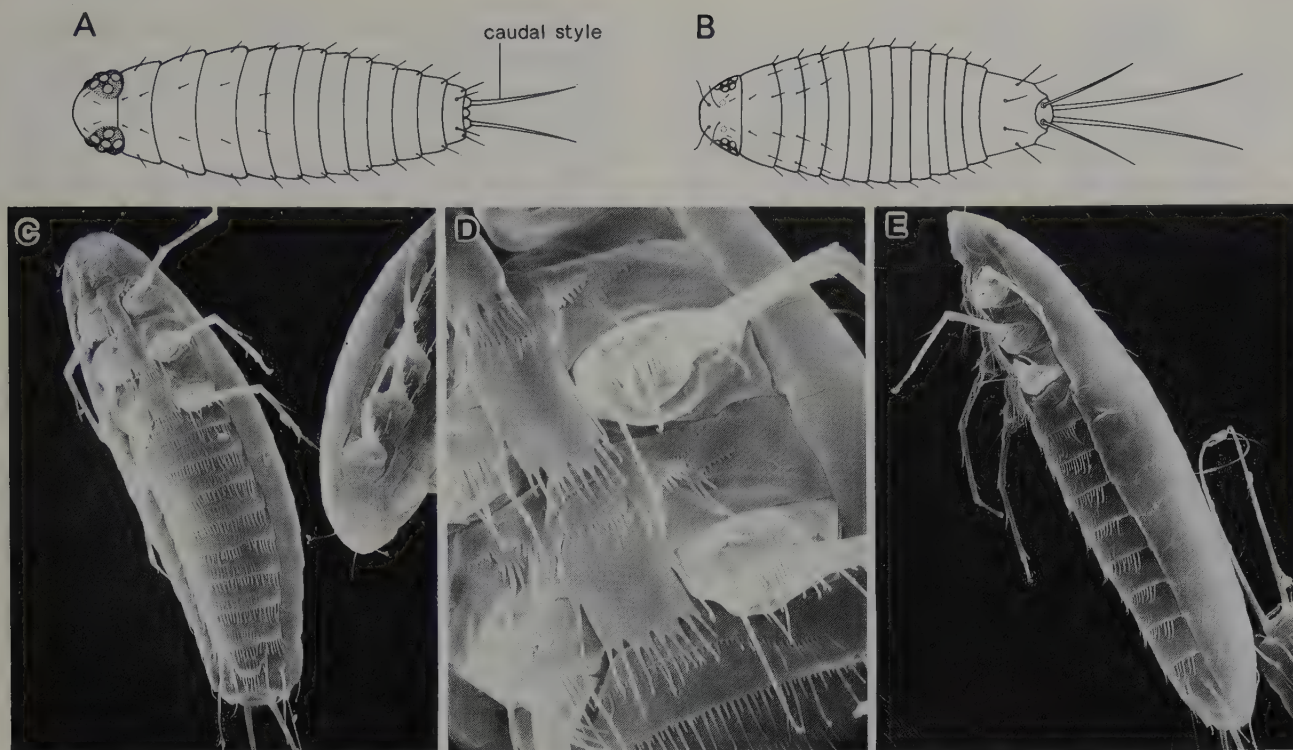


Fig. 36.5 First instar larvae: A, *Hylecthrus* sp., Stylopidae, dorsal; B, *Eoxenos* sp., Mengenillidae, dorsal; C–E, *Coriophagus riei*, Halictophagidae: C, ventral; D, thorax and abdomen, ventral; E, lateral. [A, B after Bohart 1941; C–E by B. M. Luke]

1986) and the tarsi are slender and filiform. The intercoxal sternites bear filamentous processes (Fig. 36.5D). There are long abdominal caudal setae on the 9th abdominal segment.

The 1st instar larvae of Strepsiptera are morphologically unlike the larvae of Meloidae and Rhipiphoridae (Coleoptera), although all three are often referred to as triungulin larvae. To avoid any confusion as to their similarity and hence their inclusion in the Coleoptera, Kathirithamby (1989) suggested that 1st instar larvae of Strepsiptera be referred to not as triungulins, but as Kinzelbach's primary larvae. Luna de Carvalho (1967, 1972) described a series of teratological 1st instar larvae of *Stichtotrema vilhenai* from Angola.

**Endoparasitic Larva.** When the 1st instar enters the host it moults to an apodous 2nd instar. At this stage the sexes are indistinguishable. At the 3rd instar the male differs from the female by the presence of the prolegs. At the 4th larval instar of *Elenchus tenuicornis* the female develops a distinct cephalothorax, whereas the male has a bulbous head which, after extrusion through the host cuticle, tans to form the *cephalotheca* or cap of the puparium. When the last larval instar of Mengenillidae emerges from the host for pupation it has legs, mouth and segmented abdomen.

**Pupa.** In the Mengenillidae the free-living puparium of both sexes has a mouth, legs and segmented abdomen. In Stylopidae the male pupa is exarate and adecticus. The anterior end is tanned, and the cap of the puparium (cephalotheca) has impressions of mandibles, eyes, palps and antennae (Fig. 36.6). The female pupa, which in turn

becomes a neotenic female, also has a tanned anterior end (cephalothorax).

### Biology

**First Instar Larvae.** These are produced viviparously by the neotenic female, and when they emerge they become the active host-seeking stage. Polyembryony has been recorded in *Halictoxenos*. The larvae develop over a period of time and in a fully developed female the 1st instars which are ready to emerge are found in the brood canal, whereas the embryonic stages are found within the body. Apart from the adult male the first instar larva is the only free-living stage in the Stylopidae. In the Mengenillidae both sexes are free living (i.e. they leave the host) after the late, last larval instar.

The abdominal caudal setae of the 1st instar larvae are long (usually half or a third of the length of the body) in species that use them for 'springing' movements, as observed by Kirkpatrick (1937) in the East African *Corioxenos antestiae*, by Riek (1970) in an Australian *Pseudoxenos* sp. and by O'Connor (1959) in *Stichtotrema dallatorreanum* from New Guinea. The springing movements propel 1st instars from the brood canal opening and also enable them to spring on to the host. In the Nearctic *Stylops pacificus* the caudal setae are only a fifth of the length of the body. Linsley and MacSwain (1957) found that in this species the 1st instar larvae are transported to the nest inside the crop of the bee *Andrena complexa* (Andrenidae). While in the nest, *A. complexa* regurgitates the nectar over the pollen ball and the 1st instars of *S. pacificus* are regurgitated at the same time. The cell con-



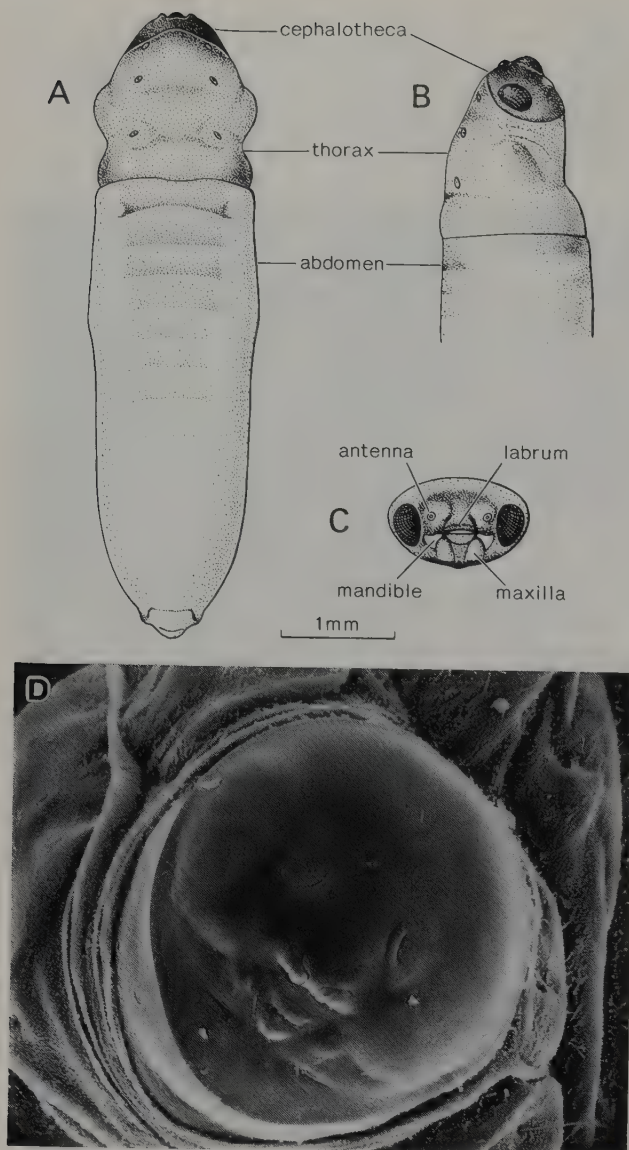


Fig. 36.6 Male puparium: A–C, Stylopidae: A, dorsal; B, lateral; C, cephalotheca, frontal; D, *Elenchus varleyi*, Elenchidae, cephalotheca, frontal. [A–C by R. Ewins; D by B. M. Luke]

taining the bee egg, food for the bee larva, and the 1st instar strepsipteran is then sealed; parasitisation begins at the egg stage. Possibly the long caudal setae occur in 1st instars of species that have to be carried to the nest or to new sites on the backs of hosts (Kathirithamby 1989), while short setae occur in species that are taken to the nests inside the crop of the host.

Sexual dimorphism is not known in 1st instar larvae, except in the family Myrmecolacidae where the male parasitises a different host (Hymenoptera: Formicidae) to the female (Orthoptera: Tettigoniidae, Gryllidae, Gryllotalpidae; Mantodea: Mantidae). Luna de Carvalho (1959), Honda (1977) and Kifune (1983) all speculated that the smaller form of the myrmecolacid 1st instar is the male and the larger form the female. G. R. Young (1987) found that when *Segestes decoratus* (Tettigoniidae)

nymphs were infected with 1st instar larvae of *Stichotrema dallatorreanum* both males and females entered the host but only the females moulted to the 2nd instar, and when *Camponotus papua* larvae were infected only the males moulted after entry.

Riek (1970) records the method of entry of *Pseudoxenos* into a *Sceliphron* larva. The 1st instar *Pseudoxenos* larva exudes a fluid in which it becomes immersed. This fluid hardens externally, but at the same time softens the cuticle of the *Sceliphron* larva. The *Pseudoxenos* larva contracts and expands while it is immersed in the fluid, as though in an effort to rupture the cuticle of the host. When the host cuticle ruptures, the *Pseudoxenos* larva enters the host and soon afterwards moults to an apodous 2nd instar larva.

First instars are more active in high light intensity such as sunlight, and less active in low light (Young 1987). Riek (1970) observed that they can rise to a height of more than 10 mm during a jump.

When stylopising exopterygote hosts (except those that live in temporary habitats, e.g. the delphacid, *Nilaparvata lugens*) the 1st instars emerge from the neotenic females and directly parasitise the nymphs which are found in the same habitat (Kathirithamby 1985).

When parasitising exopterygote hosts that live in temporary habitats, as when parasitising endopterygote hosts, the 1st instars have to be carried to nearby planted fields (Kathirithamby 1985) or to nests where they would find a nymph, larva or egg to parasitise. There have been instances where 1st instar larvae were found sitting on unstyloped hosts as e.g. *Elenchus* on *Nilaparvata lugens* (Kathirithamby 1982, 1985) and *S. dallatorreanum* on workers of *Camponotus papua* (Young 1987); this is interpreted as phoresy.

The number of 1st instars produced by the female varies according to the size of the female strepsipteran and the host. Female *Elenchus tenuicornis* parasitising *Javesella dubia* (Delphacidae) each produce about 1000 1st instar larvae, whereas female *Stichotrema dallatorreanum* in tettigoniids (*Sexava* spp.) produce about 750 000 larvae (O'Connor 1959).

**Endoparasitic Larvae.** Larvae of Strepsiptera undergo hypermetamorphosis whereby the active 1st instar larva moults to an apodous 2nd instar larva after penetrating the host. The sexes are indistinguishable at this stage.

The number of endoparasitic stages in Strepsiptera was not known with certainty until Kathirithamby *et al.* (1984), working on *Elenchus tenuicornis*, found that the cuticle of the 2nd and 3rd instars remained as a persistent sheath after deposition of the cuticle of the succeeding instar. This showed that apolysis is not followed by ecdysis and explained why exuviae of the 2nd and 3rd instars were not found in the host. In total, *E. tenuicornis* has 4 larval instars but this number might vary in other species.

Styloped delphacids and cicadellids are able to fly and are sometimes caught in aerial suction and light traps (Raatikainen 1972; Waloff 1973; Kathirithamby 1985). In passively carrying the endoparasitic stages of Strepsiptera to new locations they enable long-range dispersal of the parasite (Waloff and Jervis 1987).



**Puparium** (Fig. 36.6). In the Mengenillidae both sexes leave the host at the late larval instar to pupate externally.

In the Stylopodia only the anterior part of the body of the late last larval instar (head and prothorax in the male, Figs 36.6D, 7C; and head, pro- and mesothorax in the female, Figs 36.4F–H, 7A, B, D, E) extrude through the host cuticle.

In all Strepsiptera the last larval cuticle tans and the pupal and imaginal moulting both take place within the puparium, as in cyclorrhaphous Diptera. The adult male and female Mengenillidae emerge by discarding the cephalotheca and cephalothorax of the puparium. In the Stylopodia at the end of pupation the cap breaks in a neat circle along a preformed 'line of weakness', the structure of which is made up entirely of loosely textured endocuticle, some exocuticle and a thin epicuticle. The pharate adult inside the puparium is thought to smear a fluid that dissolves the 'line of weakness' (Kathirithamby *et al.* 1990). The thin epicuticle, at least in *E. tenuicornis*, is then broken by the slightest pressure exerted by a structure similar to the ptilinum in Diptera (see p. 718). It had been thought that the mandibles cut open the cap (Hinton 1946b; Baumert 1959) and Kinzelbach (1971a) states that in species with tooth-edged mandibles, as in the extralimital *Xenos*, the mandibles are used to open the cap. The cap breaks in a neat circle along a line of weakness and the excretion of the meconium and rhythmic pulsations enable the adult male to emerge from the puparium (Kathirithamby 1983).

Most males of Stylopodia pupate in adult hosts, but there are instances (e.g. in *Javesella dubia*) when they

pupate in nymphal hosts (Kathirithamby 1988). Delphacidae nymphs with extruded puparia do not moult to become adults (Kathirithamby 1988). Neotenic females of Stylopodia extrude only from adult hosts. Macropterous adult hosts can disperse and transport male pupae and neotenic females to new habitats.

Adult males on emergence from the puparium seek out a female; it is presumed that the virgin female attracts the male by a pheromone. Ulrich (1956) and Ross, Riek and Kinzelbach (unpubl.) were able to attract males by holding virgin females in the air. Ross (1953) was the first and only one to photograph in the field the mating of a strepsipteran (*Stylops pacificus*). Riek (1970) states that virgin females of *Coriophagus riei* parasitising *Poecilometis strigatus* (Hemiptera: Pentatomidae) attracted males for more than 4 weeks, and Kirkpatrick (1937) that *Corioxenos antestiae* parasitising *Antestia* spp. (Hemiptera: Pentatomidae) remained attractive to males for about 119 days.

The male is short lived (Linsley and MacSwain 1957; Kifune and Maeta 1975, 1978; Hirashima 1954) and flight is independent of dispersal (Waloff and Jervis 1987).

**Extrusion of the Parasite.** Stylopodia are the only insect parasitoids that keep the host alive while pupating (as in the male) or as a neotenic adult (as in the female), and in both instances the cephalotheca and cephalothorax are extruded through the host cuticle (Figs 36.4F–H, 6D, 7).

If the host is a mainly brachypterous leafhopper or planthopper, the male strepsipteran extrudes in nymphs (as in *Elenchus tenuicornis* in the U.K.), whereas if the

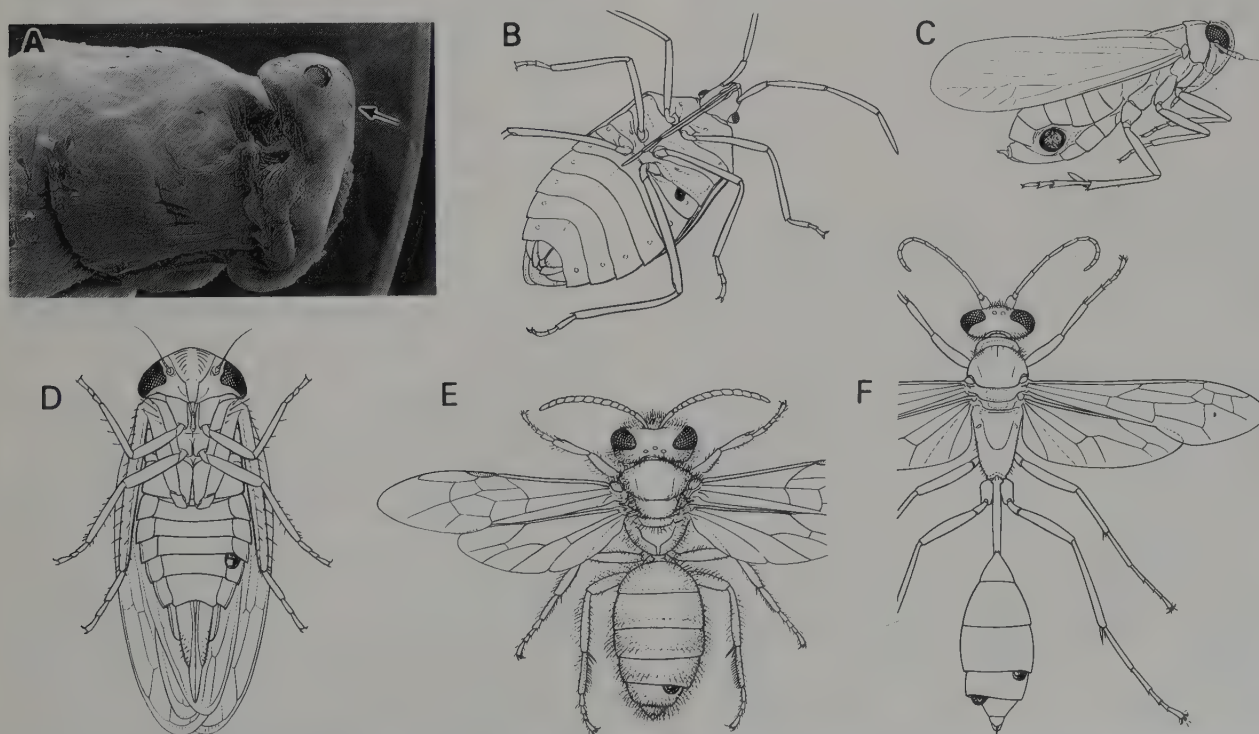


Fig. 36.7 A, B, *Coriophagus riei*, Halictophagidae, ♀ in Pentatomidae; C, *Elenchus varleyi*, Elenchidae, ♂ puparium in Delphacidae; D, *Halictophagus* sp., Halictophagidae, ♀ in Cicadellidae; E, *Hylecthrus* sp., Stylopidae, ♀ in *Euryglossa* sp. (Colletidae); F, *Pseudoxenos* sp., Stylopidae, ♂ puparium and ♀ in *Sceliphron laetum* (Sphecidae). [A by B. M. Luke; B–F by M. Quick]

host is mainly macropterous the male extrudes predominantly in adults, as in the Australian *Elenchus varleyi* (Figs 36.6D, 7C) in Brisbane (Kathirithamby 1990a); *Elenchus* sp. in Malaysia (Kathirithamby 1985) and *Elenchus tenuicornis* (Lindberg 1939; Raatikainen 1967) in Sweden. The position in the host where the parasite extrudes varies between species (Fig. 36.7).

**Superparasitism.** It is usual to find one parasite per host, but sometimes there can be more than one, with any combination of the sexes. Riek (1970) reports two or three parasites in *Bembix*, two females and two males in *Sceliphron* and 12 puparia in *Polistes*. Six *Elenchus varleyi* were found in *Sogatella kolophon*; superparasitism is common in this species but not in *Elenchus tenuicornis* in the U.K., although Raatikainen (1967) says it is considerable in this species in Sweden. A high incidence of superparasitism was found in a South African nest of *Pheidole* in which stylopisation by Myrmecolacidae was occurring. Out of 47 stylopised ants, 16 were superparasitised and 9 of these had more than two parasitoids (Kathirithamby unpubl.).

There are few instances of multiple parasitism (i.e. parasitism of one host individual by more than one species of Strepsiptera). One is of *Platybrachys* sp. (Fulgoroidea: Eurybrachyidae) from Brisbane being parasitised by *Halictophagus* and *Deinelenchus*, representing two different families of Strepsiptera. Other examples are of multiple parasitism of hosts by Dryinidae (Hymenoptera) and Strepsiptera. In *Javesella pellucida* (Fulgoroidea: Delphacidae) parasitised by *Dicondylus bicolor* and *E. tenuicornis* only 25% of the Dryinidae survived when the rival parasite was a male *Elenchus*, whereas survival was high when the rival was a female (Heikinheimo 1957; Raatikainen 1967). This was because the female lives longer than the male. When the male emerges it leaves an empty puparium and this obviously kills the host along with the Dryinidae. Abdul-Nour (1971) observed leafhoppers parasitised by *Gonatopus sepsoides* and *Halictophagus languedoci*.

**Host Specificity.** Many species of Strepsiptera are not host specific and parasitise several genera (up to 23) and species (up to 42) of hosts (Kathirithamby 1989). Specificity can extend over a genus or even a family. Riek (1970) states that in Hymenoptera specificity is high while in Auchenorrhyncha it is not. *Halictophagus* spp. are recorded from Auchenorrhyncha (Tettigometridae, Delphacidae, Eurybrachyidae, Fulgoridae, Issidae, Flatidae, Cicadellidae, Membracidae and Cercopidae) and Heteroptera (Pentatomidae and Coreidae). Among the Hymenoptera, as in Delphacidae, there is a tendency for one species of parasite to occur in all the closely related species of the host which are present in the locality.

**Effects on the Host.** Stylopisation may cause drastic changes in auchenorrhynchan hosts, particularly the Delphacidae. It has been stated commonly that stylopised Auchenorrhyncha are either 'intersexual' or sexually 'neutral' or even that stylopised hosts undergo changes to resemble the sex of the parasite (Raatikainen 1966). In those groups which have been studied closely (mainly Delphacidae), the primary (internal) and secondary

(external) sexual organs tend to be reduced or lost, and the tertiary (extragenital), found only in males, are lost. However, stylopised female leafhoppers may still be able to oviposit if they contain only very young Strepsiptera. Stylopised male Hemiptera do not develop tertiary sexual organs and superficially resemble normal females (Kathirithamby 1977–1985).

Compared to unstylopised individuals, stylopised Hymenoptera may have abnormal microsculpture, pilosity, facial coloration, antennal proportions, development of pollen-collecting organs, metasomal shape, ovipositor or male genitalia. In at least some bees the ovaries are reduced and females are sterile. Stylopised females of many Hymenoptera are male-like in some sexually dimorphic characters. [Richards 1962; Askew 1971; Clausen 1940]

Stylopised insects sometimes are much less active than unparasitised individuals, and infested wasps and bees rarely establish nests. Stylopisation does not drastically shorten the life span of the host as in most other parasitoids, and infected Delphacidae die only after emergence of the adult male, or after all 1st instar larvae have emerged from the neotenic female. This phenomenon in the Delphacidae actually prolongs the life span, since the 1st instar larvae emerge from the neotenic female contained within a stylopised host when the second generation delphacid nymphs have been produced.

**Percentage Parasitism.** In Auchenorrhyncha and bees this is usually between 10 and 20%, but can be much higher (more than 50%) in localised areas. In Hymenoptera which are solitary nesting (Sphecidae, eumenine and masarine Vespidae) percentage parasitism ranges from less than 5% to 25%, but it can be much higher in social vespids (Riek 1970).

**Other Parasites.** Rarely are stylopised insects attacked by other parasites. Riek (1970) records epipyropid larvae (Lepidoptera) in the same *Platybrachys decemmacula* (Hemiptera: Eurybrachyidae) as either *Halictophagus tryoni* or *Deinelenchus australiensis*; a mermithid nematode in a eurybrachyid with a *Deinelenchus*; and tachinid larvae (Diptera) in a pentatomid bug, *Poecilometis strigatus* with a species of *Halictophagus*.

**Natural Enemies.** Strepsiptera have occasionally been parasitised by Hymenoptera (Silvestri 1943) and Nematoda (Kinzelsbach 1971c).

**Economic Significance.** Probably Strepsiptera exert some control over the population levels of their hosts and some of these hosts are pests of economic importance. *Nilaparvata lugens* and *Sogatella furcifera* (Hemiptera: Delphacidae) and *Nephotettix* sp. (Hemiptera: Cicadellidae) are vectors of virus diseases on rice in South and South-East Asia. *Javesella pellucida* (Hemiptera: Delphacidae) is a vector of a virus disease on oats in Europe. Fruit flies (Diptera: Tephritidae) damage fruits in Australasia and *Antestia* sp. (Hemiptera: Pentatomidae) is a pest on coffee in Africa. *Segestes decoratus*, *Sexava nubila* and *Segestidea novaeguineae* (Orthoptera: Tettigoniidae) cause severe defoliation on coconuts, oil palm and *Pandanus* spp. in Papua New Guinea.



Special Features of the Australian Fauna

The Corioxenidae, Halictophagidae, Elenchidae and Stylopidae are cosmopolitan. Mengenillidae are absent from the Nearctic and Neotropical Regions, and Myrmecolacidae from the Palaearctic Region. Bohartillidae is found only in the Neotropical and Callipharixenidae only in the Oriental Region. In Australia, Mengenillidae, Corioxenidae and Myrmecolacidae are widely distributed, but the last is most abundant in the N.T. and Qld. Elen-

chidae and Halictophagidae are primarily eastern and are most abundant in areas of higher rainfall. Stylopidae that parasitise sphecids and eumenine wasps (*Pseudoxenos*) are tropical and subtropical, those from *Bembix* are found in the interior, and those from Masarinae (*Paragioxenos*) are found in S.A. and N.S.W.; although only a few stylopidised bees have been seen, they are from all over Australia, including Tas.

CLASSIFICATION

Order STREPSIPTERA  
(159 Australian spp.)

Suborder MINGENILLIDIA (20)

- 1. Mengenillidae (20)
- Mengeidae (0)

Suborder STYLOPIDIA (139)

- |                     |                         |                    |
|---------------------|-------------------------|--------------------|
| 2. Corioxenidae (9) | 3. Halictophagidae (40) | 5. Elenchidae (3)  |
| Bohartillidae (0)   | 4. Myrmecolacidae (22)  | 6. Stylopidae (65) |
|                     | Callipharixenidae (0)   |                    |

Crowson (1960, 1981) placed the Strepsiptera (as a family Stylopidae) in the order Coleoptera, within the polyphagan series Cucujiformia, near Lymexylidae. This was based on his different interpretation of the mentum, prothorax, wing venation and metendosternite. Many workers (Kinzelbach 1971a; Kinzelbach, in Hennig 1981) consider Strepsiptera to be the sister group of Coleoptera, but Kristensen (1981 and Chapter 5) has cast some doubt on their inclusion within Endopterygota. A large number of the autapomorphic features of the order are due to the endoparasitic habit of the secondary larva, the neotenic female adult of the Stylopidae and the short-lived, non-

feeding adult male, whose sole function is to seek and fertilise the neotenic female.

Kinzelbach (1971a, 1978) divided the order into nine families, one of which, Mengeidae, is known only from fossil males in the Eocene Baltic amber.

The following key to males includes only eight families, as males are not known for the South-East Asian family Callipharixenidae. The key to females contains seven families (as females are not known for the fossil family Mengeidae and the Neotropical family Bohartillidae).

Key to the Families of Strepsiptera

ADULT MALES

- 1. Tarsi 5-segmented, ending in a pair of strong claws; tarsi without sensory spots; antennae 6-7-segmented ..... 2
- Tarsi either 2-4-segmented with neither claws nor sensory spots; or 4-segmented with weak, claw-like structure and sensory spots; or 5-segmented with very weak pair of claws and sensory spots; antennae 4-7-segmented ..... 3
- 2(1). Prementum free with short palps; CuA<sub>1</sub> short, extending about to middle of wing; antennae 7-segmented with lateral flabellum on 3rd and 4th segments; fossil species only ..... Mengeidae
- Prementum fused to hypopharynx; CuA<sub>1</sub> extending almost to edge of wing (Fig. 36.8A); MA strongly developed and with anterior branch present; antennae 6-segmented with lateral flabellum on 3rd-4th or 3rd-5th segments (Fig. 36.9A) ..... Mengenillidae
- 3(1). Tarsi 2-segmented, without claws; antennae 4-segmented with lateral flabellum on 3rd (Figs 36.8E, F) ..... Elenchidae
- Tarsi 3-5-segmented, if 5-segmented ending in very weak claws; antennae 5-7-segmented with lateral flabellum on 3rd, 3rd-4th, 3rd-6th or 3rd, 5th and 6th segments ..... 4
- 4(3). Tarsi 3-segmented; antennae 6-7-segmented with lateral flabellum on 3rd, 3rd-4th or 3rd-6th segments ..... Halictophagidae
- Tarsi 4-5-segmented; antennae 4-7-segmented with lateral flabellum on 3rd, 3rd-4th, 3rd-6th or 3rd, 5th and 6th segments ..... 5
- 5(4). Mandibles absent; tarsi either 5-segmented with weak claws or 4-segmented with or without a weak claw-like structure; tarsi with sensory spots; antennae 5-7-segmented with lateral flabellum on 3rd and 4th or 3rd-6th segments (Fig. 36.8B) ..... Corioxenidae
- Mandibles present; tarsi 4-segmented, without claws or sensory spots; antennae 4-7-segmented with lateral flabellum on 3rd or 3rd, 5th and 6th segments ..... 6
- 6(5). Antennae 7-segmented with lateral flabellum on 3rd, 5th and 6th segments; maxillary base large; Neotropical ..... Bohartillidae
- Antennae 4-7-segmented with lateral flabellum on 3rd segment only; maxillary base small ..... 7

- 7(6). Antennae 4-6-segmented with broad, flat segments (Figs 36.8G, H, 9C); metathorax with spoon-shaped subalare ..... **Stylopidae**  
 Antennae 7-segmented with narrow, round segments (Figs 36.8C, D, 9B); metathorax without spoon-shaped subalare ..... **Myrmecolacidae**

## ADULT FEMALES

1. Free-living; larviform, with eyes, legs and antennae (Fig. 36.2) ..... **Mengenillidae**  
 Parasitic in host and neotenic with only the cephalothorax protruding through the host cuticle during adult stage; eyes, legs and antennae absent (Fig. 36.4) ..... 2  
 2(1). Brood canal opening apical (Fig. 36.4A); ventral side turned towards host; parasites of Heteroptera ..... **Corioxenidae** 3  
 Brood canal opening ventral and at the junction of head and thorax (Figs 36.4B-H), ventral side turned away from host  
 3(2). Head half or more as long as cephalothorax; dorsal side not membranous (Figs 36.3, 4G, H); cephalothorax semi-circular, not bell-shaped; abdominal segments 1-5 each with genital aperture; parasites of Hemiptera (Auchenorrhyncha and Heteroptera), Diptera, Orthoptera and Blattodea ..... **Halictophagidae**  
 Head less than half as long as cephalothorax, or dorsally membranous and raised above host abdominal segments; cephalothorax round, bell shaped; abdominal segments 3-6 each with genital aperture, or segments 2-3 each with 1-5 or more than 5 genital apertures ..... 4  
 4(3). Metathorax with functional spiracle; cephalothorax elongated; parasites of Heteroptera; South-East Asia ..... **Calliphari xenidae** 5  
 Metathorax without functional spiracle; cephalothorax not so elongated (Figs 36.4B-F)  
 5(4). Cephalothorax sclerotised and lying close to host abdominal segment; opening of brood canal slit-shaped (Figs 36.4B, C, 7E, F); abdominal segments 3-6 each with genital aperture; parasites of Hymenoptera ..... **Stylopidae** 6  
 Cephalothorax membranous and raised (Figs 36.4D-F); opening of brood canal wide  
 6(5). Cephalothorax with hook-like projections behind spiracles; opening of brood canal crescent-shaped (Fig. 36.4D); abdominal segments 2-3 each with more than 5 genital apertures; parasites of Mantodea and Orthoptera ..... **Myrmecolacidae**  
 Cephalothorax without hook-like projections (Figs 36.4E, F); opening of brood canal not crescent-shaped; abdominal segments 2 and 3 each with 1-5 genital apertures; parasites of Hemiptera (Auchenorrhyncha) ..... **Elenchidae**

## Suborder MENGANILLIDIA

The Mengeidae is a family known only from a single species, *Mengea tertiaria*, from Baltic amber. Only males are known. The host is unknown but Kinzelbach (1971a, b) speculates that they may have attacked Heteroptera and that females were ectoparasitic.

**1. Mengenillidae.** Kinzelbach (1971a) placed the subfamilies MENGANILLINAE, IBEROXENINAE and CONGOXENINAE in the family Mengenillidae and treated the Mengeidae as a separate family. This is the only extant family in the suborder Mengenillidia and it is distinguished from all other Strepsiptera by the presence of the free-living female imago (Fig. 36.2). In the adult male (Fig. 36.8A) the 2-segmented mandibles are well developed (Figs 36.9A) and blade-like, and the aedeagus is not hooked. Mengenillidae are parasites of Thysanura and both sexes pupate externally from the host under stones and tree-stumps. No females have been found in Australia and the males are from light traps or collected enmeshed in spider webs.

Of the 3 genera only *Mengenilla* is represented in Australia. *Eoxenos* occurs in the Mediterranean region and *Congoxenos* in Central Africa. Species of *Mengenilla* have been described from the Mediterranean region, China, the U.S.S.R. (Kazakhstan), Mongolia, Sri Lanka, Arabia and Australia, and at least one undescribed species occurs in Africa. A total of 20 species are known from Qld, W.A., the N.T., N.S.W. and the A.C.T., but only two of these, *M. gracilipes* from Bridgetown, W.A. (Lea 1910b) and *M. australiensis* from Kulgera, N.T. (Kifune and Hirashima 1983), have been named.

## Suborder STYLOPIDIA

Calliphari xenidae are known only from females and 1st instar larvae from Indonesia and Thailand; hosts belong to the hemipteran family Scutelleridae. Bohartillidae are known only from males; one species has been described from Honduras and another has been discovered recently in Dominican amber (Kinzelbach 1969, unpubl.).

**2. Corioxenidae.** Kathirithamby (1990b) divides the family into 3 subfamilies (Corioxeninae, Triozerinae and Uniclavininae) on the basis of the number of tarsi with or without claws, or with a claw-like structure in males.

Mandibles are absent in the males and the female cephalothorax is elongated and turned towards the host with a terminal brood-canal opening. Most species have been described from males attracted to light traps. Pentatomid, scutellerid, cydnid, coreid and lygaeid bugs are recorded as hosts.

### Key to the Subfamilies of Corioxenidae

#### ADULT MALES

1. Tarsi 5-segmented with claws; 3rd and 4th antennal segments each with a long lateral flabellum (Fig. 36.8B) ..... **TRIOZERINAE**  
 Tarsi 4-segmented with or without claws; 3rd and 4th or 3rd-6th antennal segments each with a long lateral flabellum ..... 2  
 2(1). Tarsi 4-segmented with a claw-like structure; Africa ..... **Uniclavininae**  
 Tarsi 4-segmented without claw-like structure ..... **CORIOXENINAE**



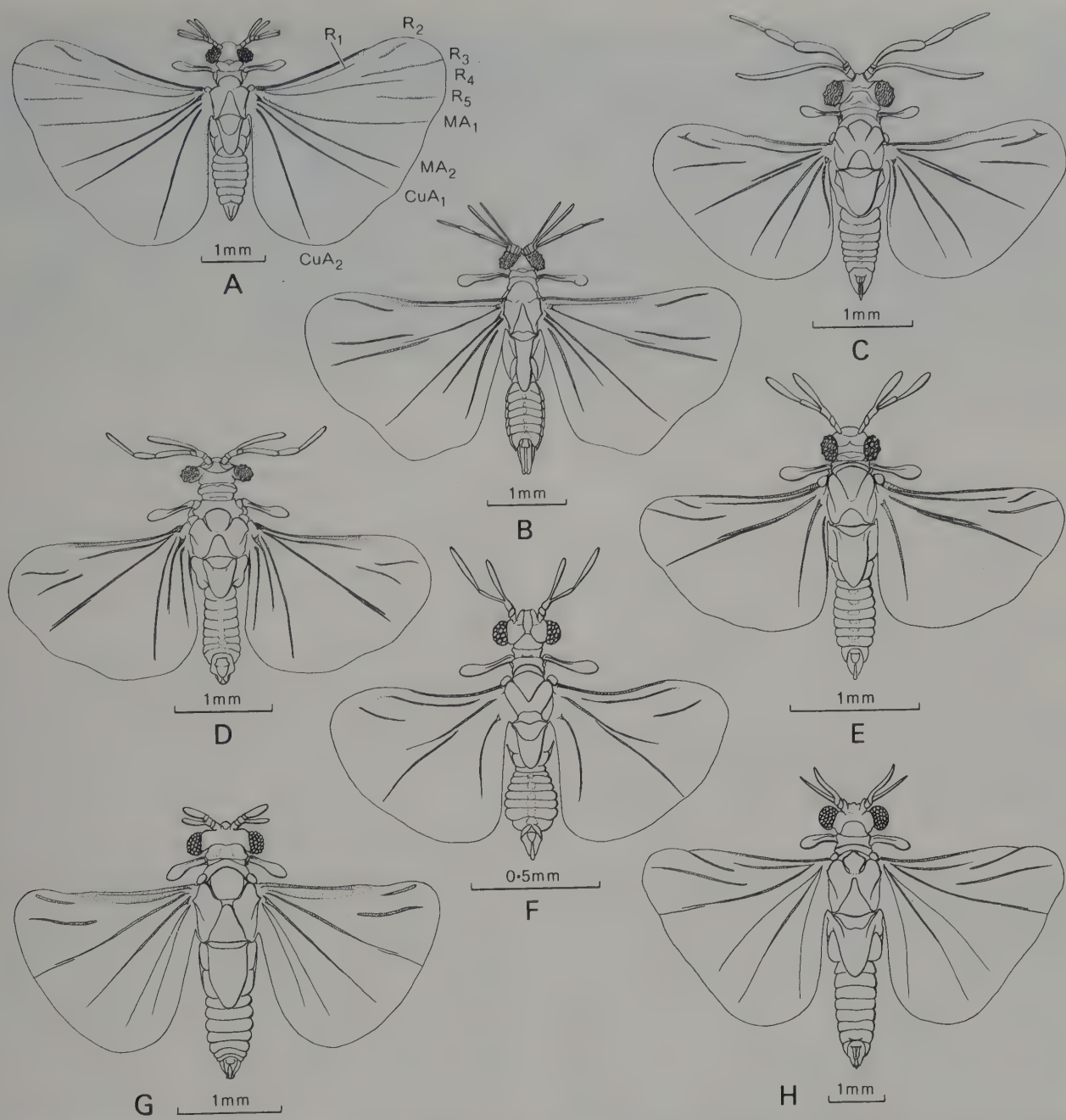


Fig. 36.8 Adult males: A, *Mengenilla* sp., Mengenillidae; B, *Triozocera* sp., Corioxenidae; C, *Myrmecolax* sp., Myrmecolacidae; D, *Lychnocolax* sp., Myrmecolacidae; E, *Deinelenchus* sp., Elenchidae; F, *Elenchus varleyi*, Elenchidae; G, *Hylecthrus* sp., Stylopidae; H, *Pseudoxenos* sp., Stylopidae. [R. Ewins]

**TRIOZOCERINAE.** One species has been described from the Australasian Region, *Triozocera papuana* from New Guinea. There are 7 species from N.S.W., Qld, W.A., the N.T. and the A.C.T. (Kathirithamby 1990b). The genus *Triozocera* is circumtropical in distribution. Known hosts belong to the family Cydnidae (Hemiptera-Heteroptera).

**CORIOXENINAE.** This subfamily is found in the West Indies, Arabia, Asia, Africa, Japan and Australia and comprises 6 genera. Its members are parasites of Heteroptera (Lygaeidae, Coreidae, Pentatomidae, Scutelleridae).

An endemic Australian genus occurs in N.S.W. (Kathirithamby 1990b).

Uniclaviniae are restricted to Africa; hosts are unknown.

**3. Halictophagidae.** Males are distinguished by their 3-segmented tarsi and 7-segmented antennae (Fig. 36.1). The number of genital openings on the anterior segments of the abdomen in the female is variable. The hosts include Auchenorrhyncha, Heteroptera, Orthoptera, Blattodea and Diptera. There are 5 subfamilies, all of which are present in Australia.

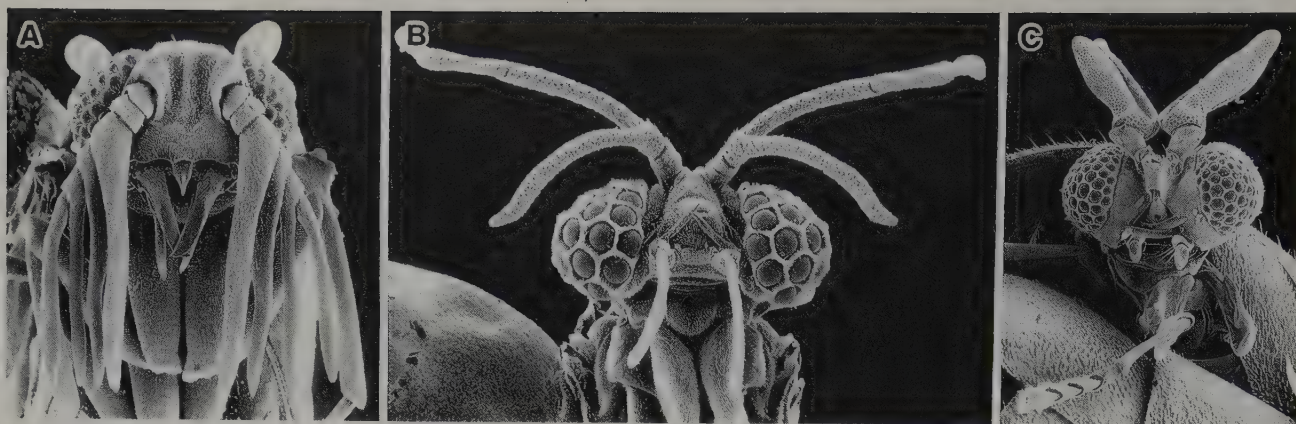


Fig. 36.9 Adult male heads, ventral: A, *Mengenilla* sp., Mengenillidae; B, *Lychnocolax* sp., Myrmecolacidae; C, *Pseudoxenos* sp., Stylopidae. [K. Pickerd]

### Key to the Subfamilies of Halictophagidae

#### ADULT MALES

1. Antennae 6-segmented with only the 3rd segment flabellate ..... DIPTEROPHAGINAE  
    Antennae 7-segmented with 3rd, 3rd–4th or 3rd–6th segments flabellate ..... 2
- 2(1). Antennae with only 3rd segment flabellate ..... TRIDACTYLOPHAGINAE  
    Antennae with 3rd–4th, 3rd–5th or 3rd–6th segments flabellate ..... 3
- 3(2). Head capsule with recognisable regions; larger species; mandibles sclerotised (Fig. 36.1B) ..... CORIOPHAGINAE  
    Head capsule simplified; mandibles not sclerotised ..... HALICTOPHAGINAE

**TRIDACTYLOPHAGINAE.** One species each has been described from China, Sri Lanka, India, the Philippines, Albania and Romania. There are 2 species in Australia, occurring in the N.T., W.A. and the A.C.T. The hosts are species of *Tridactylus* (Orthoptera: Tridactylidae).

**CORIOPHAGINAE.** Three species of *Coriophagus* occur in eastern Australia, one of which, *C. rieki* from the A.C.T., is parasitic in *Poecilometis strigatus* and *Omyta controlineata* (Pentatomidae) (Figs 36.1, 3, 7A) (Kinzelbach 1971a). Species of *Coriophagus* have been described from Nigeria, Angola, Tanzania, Zanzibar, the Solomon Islands and New Zealand.

**DIPTEROPHAGINAE.** *Dipterophagus daci* (Fig. 36.4H) is a parasite of fruit flies (Diptera: Tephritidae) and is distributed in the N.T. and Qld (Drew and Allwood 1985). Drew and Allwood erected a new family for this species, but Kathirithamby (1989) presented evidence for its inclusion in Halictophagidae.

**BLATTODEAPHAGINAE.** Only females and male pupae are known from this subfamily (Kathirithamby 1989). The hosts of the one endemic species *Blattodeaphagus beckmani* are *Platyzosteria (Melanozosteria) castanea* and *Platyzosteria (Melanozosteria)* sp. (Blattodea) from N.S.W. and northern Australia.

**HALICTOPHAGINAE** are cosmopolitan parasites of Hemiptera (Auchenorrhyncha). There are 2 genera, but only

*Halictophagus* is represented in Australia by about 32 species from W.A., the N.T., Qld, N.S.W., and the A.C.T. Host families include Tettigometridae, Delphacidae, Eurybrachyidae, Fulgoridae, Issidae, Cicadellidae, Flatidae, Cercopidae and Membracidae. Kathirithamby (1988) lists the Australian genera parasitised by *Halictophagus*.

**4. Myrmecolacidae.** This family is known mainly from males which parasitise ants (Formicidae) (Ogloblin 1939). The females parasitise Orthoptera (Tettigoniidae, Gryllidae, Gryllotalpidae) and Mantodea (Mantidae), but very few of these are known. This host dimorphism of the sexes is unique in Strepsiptera and, indeed, in insect parasitoids. Males of *Stichtotrema vilhenai* from Angola, parasitise *Crematogaster* sp. (Formicidae) and females parasitise the mantid *Sphodromantis lineola pinguis* (Luna de Carvalho 1972). Females of *Stichtotrema dallatorreanum* have been recorded from *Sexava nubila* (Orthoptera) in New Guinea (G. R. Young 1987), and one styloped queen of *Camponotus* sp. (Formicidae) with a male pupa was found in a light trap on Misima I. (Cagne unpubl.). A fossil, styloped *Camponotus* ant has been discovered recently in the Eocene oil slate of Messel (Lutz unpubl.). In a nest of *Pheidole* sp. from South Africa, 47 major and minor workers were found to be parasitised by male Myrmecolacidae (Kathirithamby unpubl.).

The segments of the 7-segmented antennae in Myrmecolacidae are narrow and rounded (Fig. 36.9B); the mandibles are knife-shaped and cross medially, the maxillae each have a small base and a long palp, and the tarsi are 4-segmented with no claws. The females are large with hooked protuberances.

The distribution of the four genera is circumtropical and Australian; there are about 22 species in Australia (N.T., Qld, N.S.W.).

**5. Elenchidae.** Elenchidae are distinguished from other Strepsiptera by their 2-segmented tarsi and 4-segmented antennae in the male; the structure of the head of the male and female; and the structure of the aedeagus (Kathirithamby 1990a).

The family is cosmopolitan and includes the genera



*Elenchus*, *Deinelenchus*, *Elencholax* and *Protelencholax*, the first two of which occur in Australia. *Elenchus varleyi* parasitises Delphacidae (Auchenorrhyncha) and occurs from the N.T. to the A.C.T. (Perkins 1905; Kathirithamby 1990a). *Deinelenchus australiensis* (Figs 36.4E, 8E), which is found from Cairns to Brisbane, parasitises Eurybrachyidae, Flatidae, Fulgoridae, Ricaniidae and Dictyopharidae. The hosts and females of *D. berrimahensis* from the N.T. are unknown.

**6. Stylopidae.** This is the largest family of Strepsiptera and has been divided by Kinzelbach (1978) into the subfamilies XENINAE, PARAXENINAE and STYLOPINAE, which parasitise Vespidae, Sphecidae and Apoidea, respectively. The males are distinguished by the 4-segmented tarsi, 4- or 6-segmented antennae (Figs 36.8G, H, 9C), metacoxae and aedeagus. The females have a flattened cephalothorax (Figs 36.4B, C) with 2–5 genital apertures.

The distribution is cosmopolitan. *Stylops*, the largest

genus in the family, is restricted to the Holarctic and is parasitic on Andrenidae. The Australian fauna contains more than 65 species in the genera *Hylecthrus*, *Halictoxenos*, *Xenos*, *Pseudoxenos*, *Paragioxenos*, and two undescribed genera, one associated with the wasp genera *Bembix* and *Bembecinus*, and the other with the bee genus *Paracolletes*. *Pseudoxenos*, which contains parasites of sphecine and eumenine wasps, is a dominant genus in Australia. *Xenos*, a dominant genus in the Neotropical Region but poorly represented in Australia, contains parasites of social wasps (Kathirithamby in press).

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# Mecoptera

(*Scorpion-flies, hanging-flies*)

G. W. BYERS

Endopterygota with head usually produced as hypognathous rostrum; first abdominal tergum fused to metanotum; usually with 2 pairs of wings, these membranous, subequal in size, with complete venation. Larvae mandibulate, eyes usually compound; pupae exarate and decticous.

The Mecoptera is a minor insect order, with about 500 known species. Nine families are recognised and five of them occur in Australia. Two families, Panorpidae and Bittacidae, include most of the known species. The Panorpidae are commonly called scorpion-flies because the bulbous, male genital segment often curves anterodorsally like a scorpion's sting. The family includes some 300 species in three genera and occurs in the northern continents and Indonesia but not in Australia. The Bittacidae are sometimes known as hanging-flies because species hang from plants by the fore legs and sometimes the mid legs. The family includes about 145 species in 17 genera. Bittacids are widespread in temperate and tropical regions, being particularly diverse in Australia and South America and comprising the entire mecopteran fauna of Africa.

The large black and reddish brown, or wholly black, species of *Harpobittacus* (Bittacidae) are the most commonly seen Australian mecopterans. Their slender, elongate body and legs, and long, narrow wings, with an expanse of 30–50 mm, give them the appearance, especially in flight, of large tipulid flies. Species of *Nannochorista* (Nannochoristidae) are sometimes common in streamside vegetation in south-eastern Australia, particularly Tas. They are small, 7–10 mm long, and have folded wings extending beyond the end of the abdomen. The wings are brown tinged and held roof-like above the body. They look like hemerobiid

lacewings. The other Australian mecopteran genera are rarely encountered.

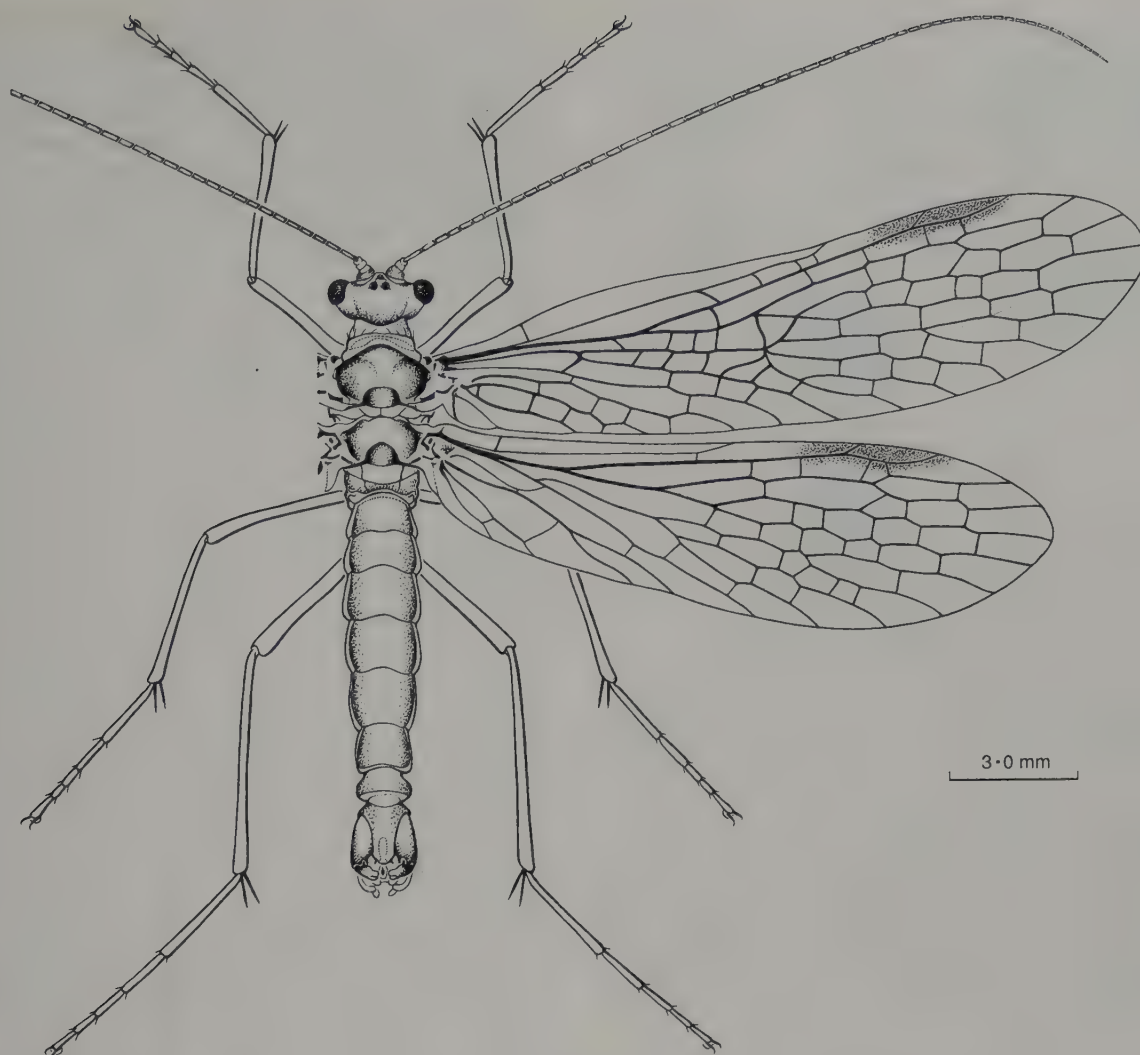
Larvae of Choristidae and Bittacidae are saprophagous and eruciform, somewhat resembling lepidopterous caterpillars. Those of Nannochoristidae are long, slender and subcylindrical; their diet includes larvae of Chironomidae. Most larval Mecoptera have compound eyes which are only rarely found in other holometabolous larvae (e.g. Micropterigidae).

Kaltenbach (1978) has provided the most recent summary of the taxonomy, morphology, physiology and behaviour of the order. Byers and Thornhill (1983) reviewed the biology.

## Anatomy of Adult

**Head** (Fig. 37.2). Hypognathous and typically prolonged below eyes; clypeus, labrum and other mouth-parts forming a rostrum; stipites usually elongate but other mouth-parts not particularly so. Compound eyes large, somewhat reduced in *Apteropanorpa*. Ocelli ordinarily 3, large in Bittacidae, small and widely separated in the extralimital Boreidae, absent in Meropeidae and Apteropanorpidae. Antennae filiform, with scape and pedicel enlarged; 14–18 elongate, slender flagellar segments in Bittacidae; 20–22 shorter, cylindrical flagellar segments in Nannochoristidae; 33–35 in the extralimital Panorpidae, to about 60 in Choristidae and Apteropanorpidae; in Meropeidae, about 25 flagellar segments,



Fig. 37.1 *Chorista* sp., Choristidae, ♂.

[T. Binder]

these short and wide near mid-length of antenna, increasingly slender toward base and apex. Mandibles short and dentate mesally in phytophagous families (Boreidae, the extralimital Panorpodidae and Eomeropidae, and probably the Meropeidae and Apteropanorpidae); somewhat longer in saprophagous Panorpidae (and possibly in Choristidae); elongate and blade-like with a single, sub-apical tooth in carnivorous Bittacidae; and short, sharp, not reaching end of rostrum and perhaps functionless in Nannochoristidae. Maxilla with setiferous lacinia, relatively bare galea (setose in Panorpidae); palp 5-segmented, usually slender but with segments 3–4 enlarged in male Choristidae (Fig. 37.2B). Paraglossae and glossae of labium reduced; labial palps 2-segmented, appearing 3-segmented in some bittacids due to elongate palpiger, greatly modified in males of Choristidae (Fig. 37.2C).

**Thorax** (Figs 1.10, 11). Cervix (neck) membranous, somewhat elongate in Choristidae, Panorpidae and Bittacidae, with well-developed cervical sclerite at each side. Pronotum saddle-like, wider than long, often with transverse ridges, sometimes enclosing mesothoracic spir-

acles in its posterolateral corners (e.g. *Apteropanorpa*, the extralimital *Boreus*). Mesothorax and metathorax usually about equally developed; scutum, scutellum and postnotum (postscutellum) distinct on both. Episterna and epimera separated by conspicuous pleural sutures, except in apterous forms such as *Apteropanorpa* that show considerable reduction and fusion of all thoracic sclerites. Sternum generally strongly infolded, with coxae in contact at ventral mid-line; coxae more widely separated in *Apteropanorpa*. Mesothoracic spiracle generally larger than metathoracic one; 1st abdominal spiracle appearing thoracic in position due to fusion of 1st abdominal segment with metathorax.

**Legs.** Coxae elongate; mid and hind coxae with large meron, except in flightless species. Femora long, slender in most families, often incrassate in male Bittacidae. Tibiae similarly long, slender, usually with 2 conspicuous, terminal spurs. Tarsi 5-segmented, basitarsus generally longest. Pretarsus with 2 claws, except in Bittacidae where single, enlarged claw and 5th tarsal segment fold against 4th to form a raptorial tarsus. Claws simple (e.g.

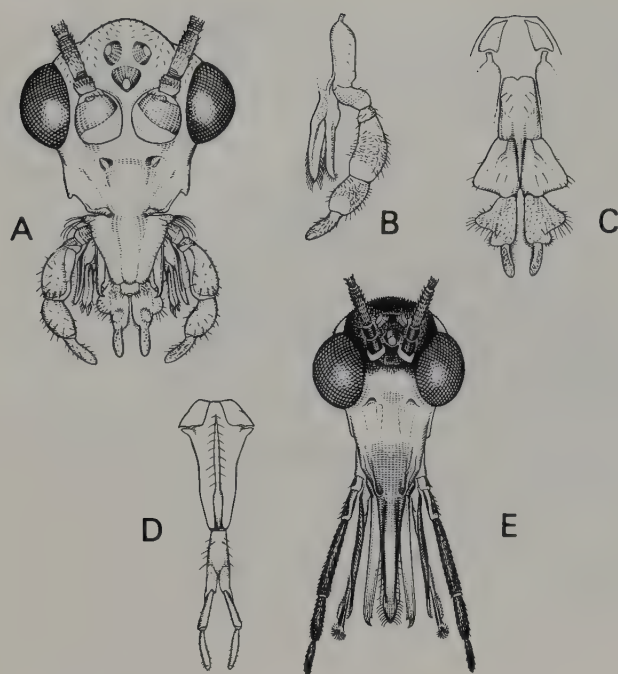


Fig. 37.2 Head and mouth-parts: A–C, *Chorista* sp., Choristidae, head frontal, maxilla ventral, labium ventral; D, E, *Harpobittacus*, Bittacidae, labium ventral, head frontal. [M. Quick]

*Apteropanorpa*), with single basal tooth (*Nannochorista*), or pectinate (Choristidae, Panorpidae, *Austromerope*).

**Wings** (Fig. 37.5). Fore and hind wings similar in size and shape, usually membranous but sclerotised and hook-like in Boreidae, absent in *Apteropanorpa* and *Apterobittacus* (California), reduced in flightless *Anomalobittacus* (South Africa) and many females of

Panorpodidae. Shape varies from elongate and narrow, especially in basal one-third (5.5 times as long as greatest width in *Harpobittacus*), to broad (about 2.7 times as long as wide in *Meropeidae*). Membrane without distinct markings other than stigma, in Australian genera, except *Symbittacus* from northern Qld. Transverse banding or large spots common on wings of Panorpidae and several tropical genera of Bittacidae. All major longitudinal veins and their branches present; cross-veins few (*Nannochoristidae*) to numerous (*Austromerope*). Fore and hind wings not effectively coupled in flight; jugal lobe of fore wing and base of costa of hind wing with stout setae (resembling frenulum of Lepidoptera).

**Abdomen.** Eleven-segmented, with T1 fused to metathorax (Fig. 1.20); S1 free, often divided into 2 sclerites. In Bittacidae, abdomen elongate, slender, subcylindrical; expanded in posterior one-third to one-half in females, depending on egg content; enlarged beyond 7th segment in male. Abdomen of female in other families slightly constricted at attachment to thorax, widest near mid-length, tapering apically. Segments 7 and 8 abruptly more slender than 2–6 or enlarged genital bulb (segment 9) in males of Panorpidae; their diameter only slightly reduced in remaining families. Cerci arising between T10 and T11; in females 1-segmented in Bittacidae and Boreidae, otherwise 2-segmented but with bases suggesting third segment in Choristidae and Panorpidae; in males 1-segmented, small in most families, elongate in some Bittacidae (e.g. *Tytthobittacus*), absent in *Apteropanorpidae* and Boreidae.

External genitalia of females (Fig. 1.24c) consisting of a subgenital plate (sometimes divided medially) beneath gonopore and, in most families, a sclerotised structure surrounding entrance to spermathecal duct on S9. T10

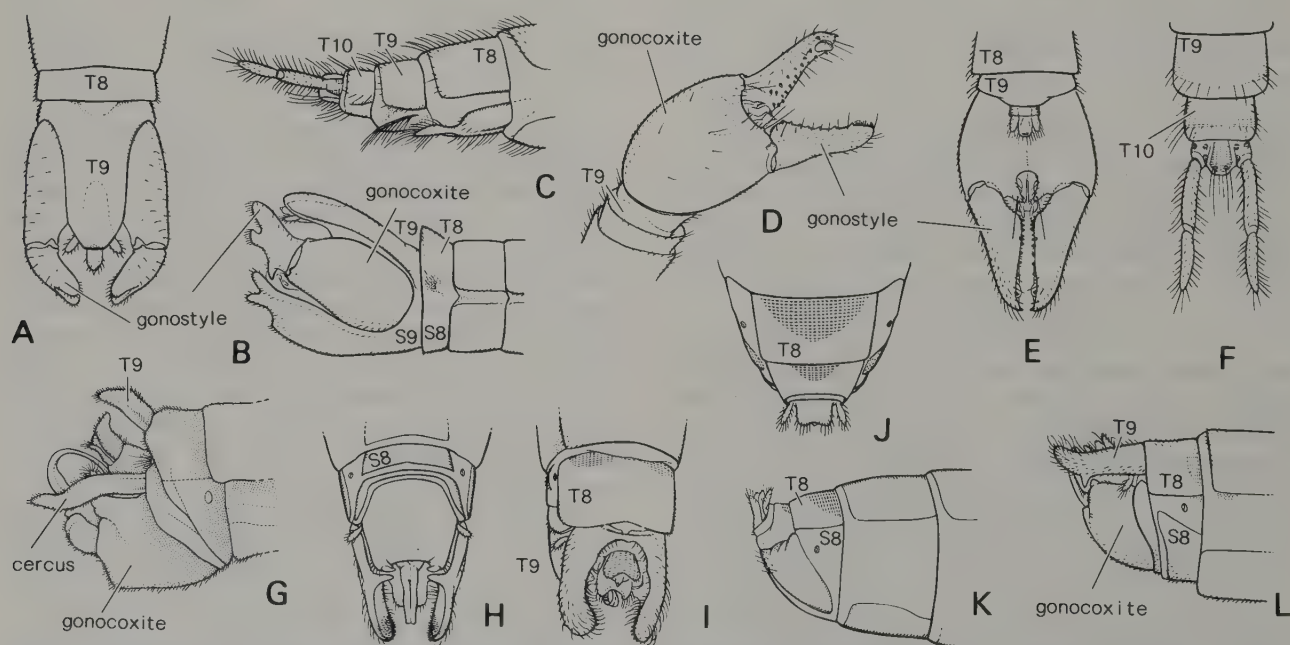


Fig. 37.3 Terminalia: A, B, *Chorista* sp., Choristidae, ♂ dorsal, ♂ lateral; C–F, *Nannochorista* sp., Nannochoristidae, ♀ lateral, ♂ ventrolateral, ♂ dorsal, ♀ dorsal; G, *Tytthobittacus* sp., Bittacidae, ♂ lateral; H–L, *Harpobittacus* sp., Bittacidae, ♂ ventral, ♂ dorsolateral, ♀ ventral, ♀ lateral, ♂ lateral.

[A–F, H–L by M. Quick; G by T. Nolan]



prolonged and cerci pointed and sclerotised in Boreidae, to form a functional ovipositor.

In males abdominal segments 6–9 (Panorpidae), 7–9 (Apteropanorpidae), 8–9 (Choristidae), 9 only (Bittacidae and Nannochoristidae), completely sclerotised (i.e. without membranous pleura). T9 and S9 prolonged caudad above and below basistyles in Choristidae and Panorpidae (Figs 37.3A, B); in Bittacidae only tergum extended forming 2 elongate, generally compressed, variously shaped epiandrial lobes (Figs 37.3H, I, L, T9). Basistyles (gonocoxites, gonobases) enlarged, broadly fused basally, except elongate and separated in Meropeidae, almost completely fused in Nannochoristidae. Dististyles (gonostyles, claspers) variable in size and shape: small and simple lobes in most Bittacidae; cheliform with numerous blackened denticles on mesal surfaces in Nannochoristidae; branched and complex in Choristidae; long, slender and nearly straight in *Austromerope*. Aedeagus a simple, tapering, curved (sometimes coiled) tube in Bittacidae; short and slender in Meropeidae; highly complex with variously sclerotised, attached parameres in Choristidae, Panorpidae and Eomeropidae.

**Internal Anatomy.** Oral cavity elongate, pharynx short, muscular, forming a pharyngeal pump in families having a nearly liquid diet; oesophagus of variable length. Proventriculus muscular, largely lined with hair-like acanthae. Ventriculus (mid gut) of much greater diameter than other parts of digestive tract, elongate (from about one-fourth length of entire tract in Meropeidae and Choristidae to two-thirds in Bittacidae). Intestine slender, with 6 Malpighian tubules; rectum somewhat expanded, with 6 rectal papillae for water resorption (except in Boreidae). Salivary glands tubular, paired, 2-branched, slender in female, much enlarged in male Panorpidae (see Biology). Central nervous system comprising brain, suboesophageal ganglion, 3 thoracic ganglia and 5–8 abdominal ganglia, 1st abdominal ganglion usually partially fused with metathoracic ganglion, last somewhat enlarged; males usually with one more abdominal ganglion than females. In males testes paired, each with 3 (e.g. the extralimital *Panorpa*) or 4 (*Harpobittacus*) fusiform follicles; vasa deferentia elongate, often compactly coiled (epididymis) for part of their length, joining median seminal vesicle. In females ovaries paired, with variable number of sequentially arranged polytrophic ovarioles (7 in *Chorista*, 8–10 in *Bittacus*, 10–13 in *Panorpa*, 6–10 in *Boreus*); accessory glands elongate, paired, often joined basally; single, large spermatheca with long, slender, greatly coiled duct. Eversible pheromone-dispersing vesicles between T6 and T7 and T7 and T8 in most male Bittacidae, in ventral concavity of genital bulb in Panorpidae and apparently in Panorpididae; so far unknown in other families.

### Immature Stages

**Egg.** In Choristidae, Nannochoristidae, Panorpidae, Panorpididae and Boreidae, eggs ovoid; chorion smooth to finely reticulate (some *Panorpa* species). In most Bittacidae, eggs at oviposition cuboidal or with triangular ends, surfaces slightly impressed; chorion thickened,

tough or hardened. Eggs of bittacids become subspherical shortly before hatching.

**Larva** (Fig. 37.7). In Panorpidae, Bittacidae, Choristidae and Apteropanorpidae, larvae are eruciform with a well-sclerotised head capsule, subconical thoracic legs and fleshy prolegs on the first 8 abdominal segments. Larvae of Nannochoristidae are elongate, 16–20 times as long as their greatest diameter, subcylindrical but tapering posteriorly, with slender legs and no abdominal prolegs. Those of Boreidae and Panorpididae are scarabaeiform, with mid and hind legs extending somewhat laterad and prolegs are absent. Immature forms of Meropeidae and Eomeropidae are unknown. Compound eyes with 30 or more ommatidia in Choristidae and Panorpidae, only 7 in Bittacidae, usually 3 in Boreidae and none in Panorpididae. While the larva of *Nannochorista* has 16 ommatidia in each eye, that of the closely related New Zealand genus *Microchorista* has only a pair of pigmented eye-spots. One median-frontal ocellus in Bittacidae and Choristidae. Pronotum more densely sclerotised than other thoracic terga, saddle-like, often enclosing mesothoracic spiracle posterolaterally. Two rows of 3-branched, fleshy dorsal processes on mesothorax to 9th abdominal segment in Bittacidae (Fig. 37.7H); less prominent processes along sides. Conical projections each bearing an annulated seta similarly arranged in 1st instar Choristidae and Panorpidae; these absent in later instars except persisting on abdominal segments 8 and 9 in Panorpidae. Tenth (anal) segment with eversible papillae forming a suction organ; larvae can cling to the substrate by this structure and elevate the anterior end of the body. In Nannochoristidae, the abdomen terminates in a pair of sclerotised hooks and elongate dorsal and ventral anal papillae (Pilgrim 1972). Larvae usually peripneustic.

**Pupa** (Fig. 37.4). Adult-like; exarate, wings compactly folded in sheaths. Rostrum less prolonged than in adult. Decticious; mandibles larger, more larval- than adult-like.

### Biology

**Adults.** Most Mecoptera inhabit moist environments, but species of semi-desert habitats are known (Byers and



Fig. 37.4 Pupa of *Harpobittacus* sp., Bittacidae.

[M. Quick]



Thornhill 1983). Some species of *Harpobittacus* may be found under fairly dry conditions, while other Australian species of all genera are restricted to mesic environments, and *Nannochorista* is never far from open water.

Bittacids occur in leafy, herbaceous vegetation or low shrubs and less often in tall grass. They hang by their fore legs and capture other insects with the hind tarsi, or they may hunt actively using sweeping movements of the hind legs as they fly up plant stems. Soft-bodied insects such as flies, moths, bees and various larvae, as well as spiders, are usual food. *Harpobittacus* often takes nectar as it forages for prey on blossoms of such shrubs as *Leptospermum*, in spring (Riek 1970). Bornemissza (1966a) observed that in *Harpobittacus australis* and *H. nigriceps* only the males captured prey and that females obtained nourishment by way of nuptial offerings from males. Female bittacids in other parts of the world, however, have often been collected with prey, and Smithers (1973) reported a few such instances from eastern Australia. When disturbed, bittacids usually fly slowly and only a few (3–4) metres before again suspending themselves in vegetation.

Adults of *Harpobittacus* are found from spring to autumn, those taken in the autumn being in general larger and darker than spring individuals of the same species, suggesting two generations per year (Riek 1970). That the wings of autumnal adults often have tattered margins, however, suggests a long adult life. Bornemissza (1966b) found that while average adult life in the laboratory was 15 days, some marked individuals lived more than 35 days in their natural habitat. Associated with herb-shrub habitat in moist, low-lying areas in spring, *Harpobittacus* species later spread into other habitats, from which females return to oviposit.

The Choristidae are mainly autumnal and locally common in tall grasses or broad-leaved herbs near small streams. Riek (1970) noted that 'they make short darting flights'. Adults of *Nannochorista* have two periods of emergence, in late spring and again in autumn so that there are two generations per year as in *Panorpa* in many parts of North America. The diet of adults of both *Chorista* and *Nannochorista* is unknown. Mandibular structure, however, suggests that *Chorista* is herbivorous or possibly saprophagous and that *Nannochorista* has a liquid diet.

**Reproduction.** Males in many genera (e.g. *Harpobittacus*, the extralimital *Bittacus* and *Panorpa*) emit pheromones which draw females from several metres distance. Thereafter, a nuptial meal usually is offered by the male. This has been best documented in Bittacidae, in which the meal is a prey insect (Bornemissza 1966b; Thornhill 1976). In some species, the prey is transferred to the female during mating, while in others it is retained in the grasp of the male's hind tarsi as the female feeds. Mating of *Panorpa* may take place at a food source, usually a dead insect, or the male may secrete a short pillar of saliva which becomes gelatinous in air and which is attractive to the female. Riek (1970) noted that in the copulation of *Chorista*, with male and female side-by-side, 'the mouths of the pair touch, and

there is a very evident and persistent exchange of fluids'. Mating in *Harpobittacus* may last 3–10 minutes, rarely longer, and a male may secure prey and then mate several (6–8) times a day, occasionally using a large prey item more than once. During mating, the male grasps the female with his tarsi as well as by his genital appendages. In Panorpidae, the costal margin of the female's fore wing is clamped in a structure on T3 and T4 of the male to prevent separation. In most genera, mating pairs are not easily distracted, even when touched.

Sex determination is of the XO type in nearly all Mecoptera. The haploid number of chromosomes in *Chorista australis* is  $14+X(O)$ , for *Nannochorista* species  $9+X(O)$  and  $13+X(O)$  (Bush 1967); it is not known for *Harpobittacus* but is  $15+X(O)$  in some species of Bittacus.

**Immature Stages.** Female Bittacidae simply drop their eggs to the ground. The eggs have a hard or tough chorion that resists desiccation and hatching follows a dormant period varying from a few weeks to several months. Choristidae, like Panorpidae, oviposit clusters of several to many eggs in pre-existing cavities in moist soil. Eggs of *Chorista* hatch in 12–15 days. *Nannochorista* lays up to 25 eggs end-to-end on wet leaf litter near the water's edge. *Boreus* places its eggs singly or in small clusters near the bases of stems of moss on which the larvae will feed. Eggs of most Mecoptera absorb water from the substrate and increase 38–100% in dimensions.

In life histories that have been studied, there are four larval stages, a prepupal stage in which the 4th instar larva is quiescent, and a pupal stage. *Harpobittacus australis* was reared from egg to adult by Currie (1932, as *H. tillyardi*). Larvae readily consume dead insects and reach full size in about a month. When full grown, each larva excavates a more or less vertical cell in the uppermost soil and there spends a 5–6 month prepupal stage. The pupal stage lasts 14–50 days. Larval bittacids of all genera, as far as is known, thickly coat their dorsal processes with their own faeces and soil particles. Pilgrim (1972) found that the first three instars of the aquatic *Microchorista* are apneustic. The hemipneustic, 4th instar larva leaves the water and may excavate a cell or enter an appropriate cavity in damp vegetation (e.g. in moss), in soil, or even beneath the bark of a partially-submerged log, within 20 cm of water's edge. Although the mature larva is over 17 mm in length, the pupa is only about 5 mm long and has the general shape of the adult.

**Natural Enemies.** Web-building spiders are probably the most important predators of adult Mecoptera, although some species of *Panorpa* are known to succeed in stealing prey from spiders' webs. Large opportunistic insect predators occasionally capture mecopterans. *Harpobittacus* sometimes preys on *Chorista* and is in turn fed upon by large asilid flies or reduviid bugs. There are no Australian records of parasites or of predation by vertebrates.

**Economic Significance.** Mecoptera are usually of minimal economic importance. Predatory adults of *Harpobittacus* may become abundant enough to have considerable impact on population levels of some of their



various prey species. For example, an attempt to control ragwort with the introduced cinnabar moth, *Tyria jacobaeae*, was foiled in part by heavy predation (up to 100% locally) on the moth caterpillars by *Harpobittacus nigriceps* (Bornemissza 1966a).

### Special Features of the Australian Fauna

The most striking aspect of Australia's Mecoptera is that virtually all belong to endemic genera. While the Bittacidae are nearly world-wide in distribution, with the genus *Bittacus* occurring on five continents besides Australia, all but one of the Australian species belong to

five endemic genera, of which four include but a single species. The Choristidae occur only in south-eastern Australia. Neither Choristidae nor Bittacidae are represented in New Zealand. The one known species of Apteropanorpidae is limited to Tas. A widespread Palaeozoic or early Mesozoic distribution of ancestral Meropeidae would best account for the present disjunct range of that family. Nannochoristidae include half a dozen species of *Nannochorista* equally divided between south-eastern Australia and southern South America, and a single species of *Microchorista* in New Zealand. There are no faunal connections in Mecoptera between Australia and South-East Asia or Indonesia.

### CLASSIFICATION

#### Order MECOPTERA (27 Australian species)

- |                         |                         |                    |
|-------------------------|-------------------------|--------------------|
| 1. Nannochoristidae (3) | 3. Meropeidae (1)       | 5. Choristidae (8) |
| 2. Bittacidae (14)      | Eomeropidae (0)         | Panorpididae (0)   |
| Boreidae (0)            | 4. Apteropanorpidae (1) | Panorpidae (0)     |

This classification is based upon phylogenetic studies by Willmann (1987). Differences of opinion exist on how the families are related phylogenetically. The recognition of two or three suborders (Protomecoptera, Eumecoptera,

Neomecoptera) has no particular utility and probably little basis in morphology or in the fossil record. Smithers (1987) summarised the Australian fauna and provided a key to the Australian genera and species.

#### Key to the Families of Mecoptera Known in Australia

##### ADULTS

1. Tarsi raptorial, each with a single claw immovably joined to 5th tarsal segment, which closes against 4th (Fig. 37.8); wings elongate, slender in basal one-third (Figs 37.6B, C) ..... **Bittacidae**
- Tarsi not raptorial, each with 2 small claws; wings, if present, not conspicuously slender in basal one-third ..... 2
- 2(1). Wings absent; mesothoracic and metathoracic sclerites small, fused together, with sutures obliterated (Fig. 37.9) ..... **Apteropanorpidae**
- Wings present; thoracic sclerites not reduced or fused, sutures distinct ..... 3
- 3(2). Venation reticulate, with about 15 costal cross-veins between C and Sc (Fig. 37.6A); M in fore wing with more than 6 branches reaching wing margin; body slightly depressed, wings folded flat over abdomen in repose ..... **Meropeidae**
- Fewer than 8 costal cross-veins (Figs 37.5A–C); M in fore wing with 5 or fewer branches; body not depressed, wings held roof-like over abdomen in repose ..... 4
- 4(3). In fore wing Rs 3-branched (Fig. 37.5C), M 4-branched; cross-veins not numerous (e.g. only 3 within radial field) ..... **Nannochoristidae**
- In fore wing Rs 4-branched (Figs 37.5A, B); M usually 5-branched; cross-veins numerous (15 to 30 in radial field) ..... **Choristidae**

##### LARVAE (The larvae of Meropeidae are not known.)

1. Body elongate, slender, about 16–20 times as long as greatest diameter (Fig. 37.7A); abdomen smooth-surfaced, without prolegs; aquatic ..... **Nannochoristidae**
- Body eruciform, about 7 times as long as greatest diameter; abdomen with prolegs and with small or conspicuous dorsal and lateral processes; terrestrial, in soil, leaf litter or bryophytes ..... 2
- 2(1). Thoracic and abdominal segments bearing conspicuous paired, fleshy dorsal processes (Fig. 37.7H), each terminating in 3 spatulate or acuminate setae; abdominal prolegs smaller than dorsal processes ..... **Bittacidae**
- Thoracic and abdominal segments without conspicuous dorsal processes; some single setae may have thickened bases but these never as long as abdominal prolegs ..... 3
- 3(2). Abdominal prolegs blunt, thicker at base than thoracic legs and more than half as long as legs (Fig. 37.7E) ..... **Choristidae**
- Abdominal prolegs slender, acutely pointed, about one-third length of thoracic legs ..... **Apteropanorpidae**

**1. Nannochoristidae.** This ancient family occurs in Australia (*Nannochorista*, 3 or 4 spp.; N.S.W., Vic., Tas.), New Zealand (*Microchorista*, 1 sp.) and South America (*Nannochorista*, 3 spp.). Adults are small (fore wings

5.5–8.5 mm), the wings tinged with brown, unmarked or with greyish brown bordering most cross-veins. Venation reduced (Fig. 37.5C) with fewer cross-veins than in other families and Rs apparently only 3-branched ( $R_2$  possibly

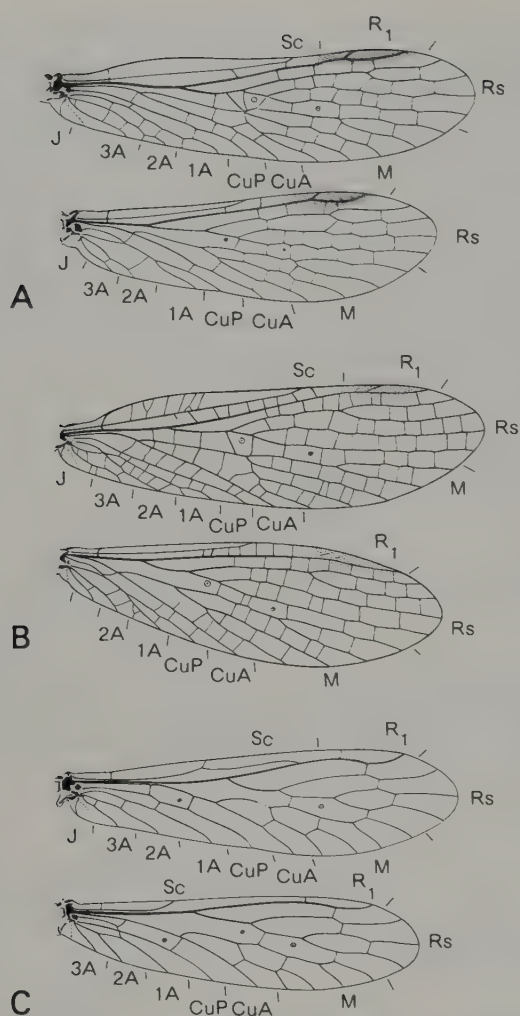


Fig. 37.5 Wings: A, *Chorista* sp., Choristidae; B, *Taeniochorista* sp., Choristidae; C, *Nannochorista* sp., Nannochoristidae. [M. Quick]

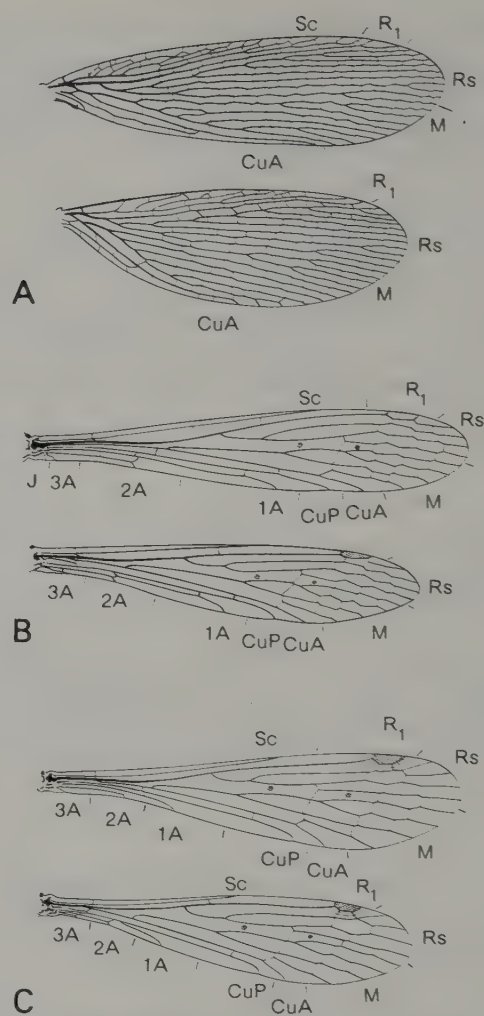


Fig. 37.6 Wings: A, *Austromerope* sp., Meropeidae; B, *Harpobittacus* sp., Bittacidae; C, *Austrobittacus* sp., Bittacidae. [M. Quick]

joining  $R_1$  as a cross-vein). Rostrum short, slender, with mandibles not reaching the acute apex. Compound eyes relatively large, protruding. Basistyles of male broadly joined medially; dististyles cheliform. S8 and S9 of female divided by median membranous zone. Larvae elongate, slender (Figs 37.7A–D), with 2 caudal hooks; eyes compound in *Nannochorista*, simple in *Microchorista*. Adults in low vegetation near streams and lakes. Larvae aquatic, occurring in accumulations of silt in shallow, slow streams, carnivorous, feeding on larval chironomids and probably other larval Diptera. Riek (1954e) provided a key to the Australian species. Pilgrim (1972) described the larva, pupa and habitat preferences of *Microchorista* (as *Choristella*).

**2. Bittacidae.** These are the most commonly collected Australian Mecoptera. They are large (fore wing 17.5–26 mm in *Harpobittacus*, 14–16.5 mm in other genera) and by suspending themselves in leafy vegetation and carrying prey in flight are more conspicuous than other mecopterans. The family is widespread, with numerous species in tropical and temperate regions.

Single-clawed, raptorial tarsi (Fig. 37.8). Wings elongate, slender basally (Figs 37.6B, C). Compound eyes large, protruding; ocelli large, on a median prominence; rostrum slender. Basistyles of male bulbous, broadly fused ventrally; dististyles ordinarily small, inconspicuous; T9 divided into 2 lobes, clasper-like in appearance but not in function. Larvae with 2 dorsal rows of branched, fleshy processes (Fig. 37.7H).

Riek (1954e, 1970) recognised 2 species groups of *Harpobittacus*: the *australis* group, characterised by an apical cross-vein between CuP and 1A and occurring in somewhat dry habitats, and the *nigriceps* group, lacking the apical cross-vein and living in more mesic environments, often along streams. In various parts of Australia, a representative of each group may occur. There are 10 species of *Harpobittacus*, 2 in south-western W.A., the others ranging from central Qld to eastern S.A. and Tas. Other Australian genera are *Austrobittacus* and *Edriobittacus* from coastal Qld (near Rockhampton and southward); *Tythobittacus* (Blue Mountains and near Gosford, N.S.W.); and *Symbittacus* (near Cairns, northern



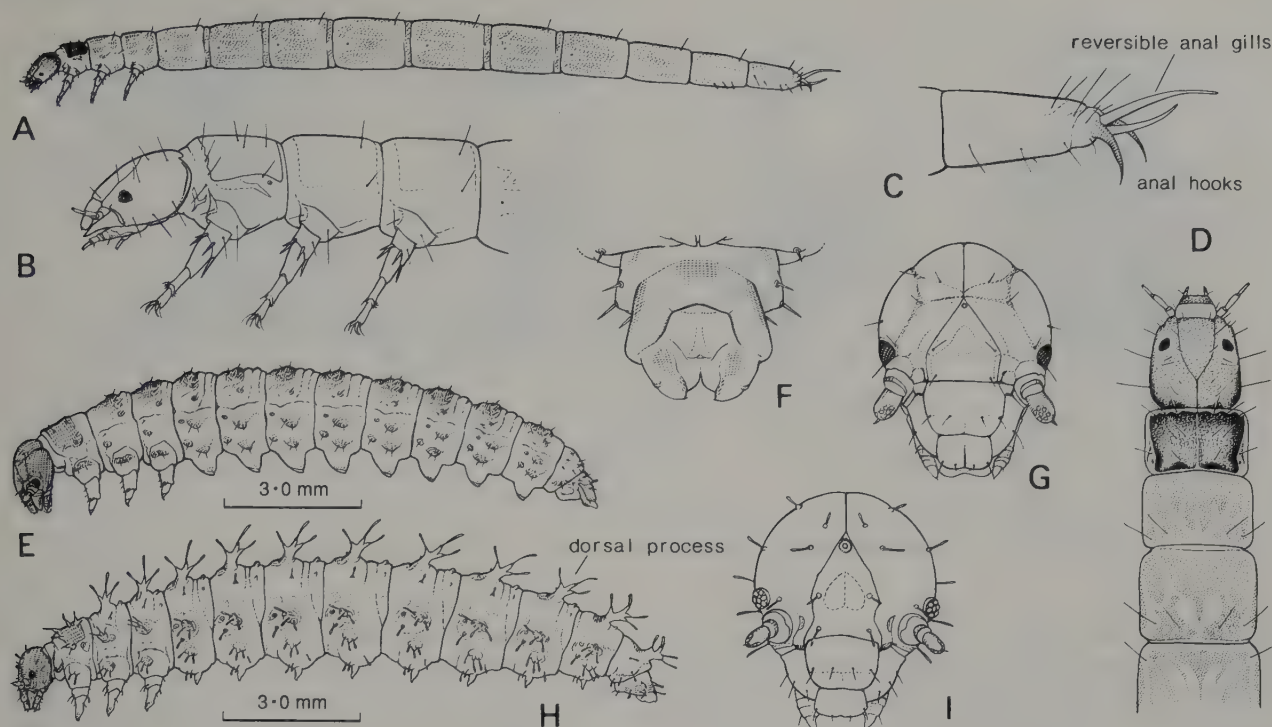


Fig. 37.7 Larvae: A–D, *Nannochorista* sp., Nannochoristidae; E–G, *Chorista* sp., Choristidae (F, apex of abdomen, ventral); H, I, *Harpobittacus* sp., Bittacidae. [M. Quick]

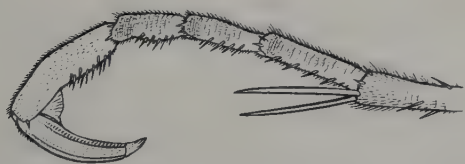


Fig. 37.8 Tarsus of *Harpobittacus* sp., Bittacidae.

[M. Quick]

Qld). Byers (1986) and Smithers (1987) provided keys to Australian genera and species.

**3. Meropeidae.** Only 2 species are known in this small, geographically disjunct family. *Austromerope poultoni* has been collected only in the vicinity of Perth, W.A., beneath objects on the ground (log, rock) and in pitfall traps (Faithfull *et al.* 1985; Smithers 1988). *Merope tuber* is widespread but uncommon in the eastern half of North America (Byers 1973).

Relatively broad, brown-tinged wings held overlapped and flat above the abdomen, and the opisthognathous head partially concealed by the pronotum, give these secretive insects a cockroach-like appearance. The antennae are only about one-fourth of the wing length and thickened in the basal half; eyes reniform. Wings with multiple branchings of R and M and numerous cross-veins (Fig. 37.6A). In males, the genital appendages are nearly as long as the rest of the abdomen.

**4. Apteropanorpidae.** *Apteropanorpa tasmanica* (Fig. 37.9) is wholly wingless and superficially resembles subapterous Boreidae of the northern continents. Like the boreids, it occurs in mossy habitats, and adults may be found on snow. Adults have been collected at high elevations in Tas., in May and September. J. W. Evans (1942) described from moss an eruciform larva that is probably of this species.

**5. Choristidae.** This wholly Australian family is readily recognised by wing structure: vein C bows forward in the fore wing, creating a wide costal cell, and there are numerous cross-veins (Figs 37.5A, B). *Chorista* and *Neochorista* typically have no cross-veins in cell C

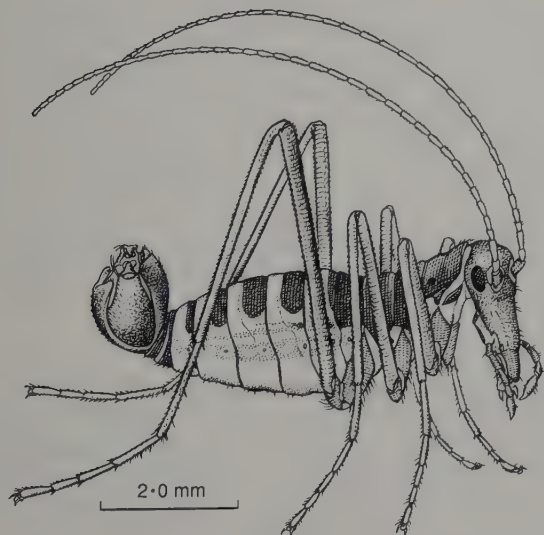


Fig. 37.9 *Apteropanorpa tasmanica*, Apteropanorpidae, ♂. [M. Quick]

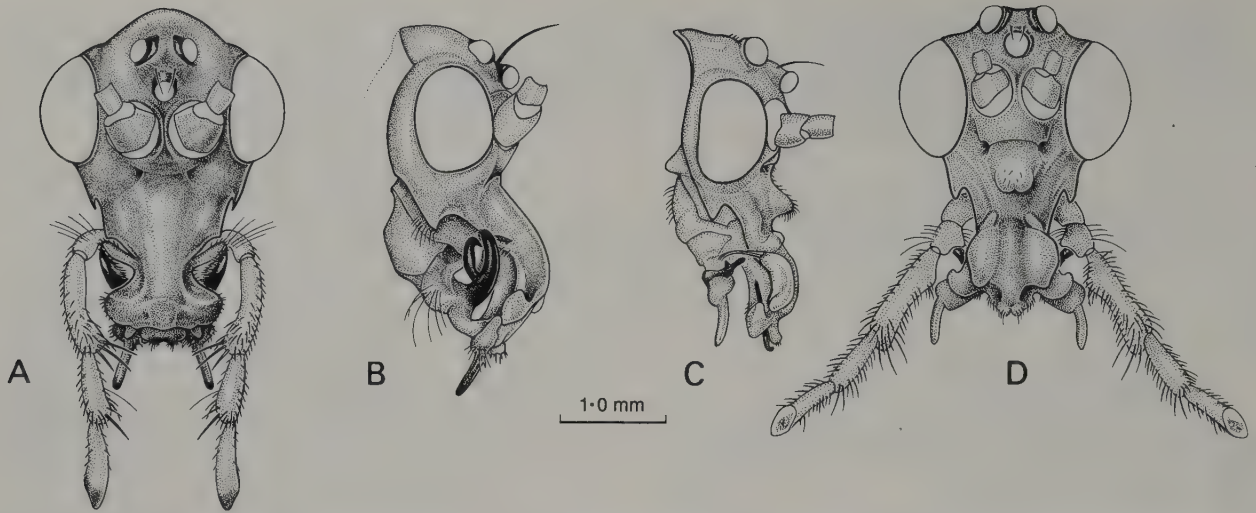


Fig. 37.10 Head of Choristidae: A, B, *Neochorista ruficeps*; C, D, *Taeniochorista pallida*. Frontal and lateral; maxillary palps removed from B and C.

[A. Hastings]

beyond the humeral vein, while *Taeniochorista* has 3–6. In males, the rostrum and particularly the maxillary and labial palps are highly modified (Figs 37.10A–D), providing good characters for species recognition (Riek 1973a). *Chorista* and *Neochorista* range from south-central Vic. to eastern N.S.W., from the coast to about 200 km inland. *Taeniochorista* occurs from south-eastern

Qld to near Sydney, N.S.W. Known larvae have transverse bands of short setae on most segments, stout prolegs, and many-faceted, compound eyes (Fig. 37.7E); they occur in surface soil and leaf litter and are saprophagous. The mature larva excavates a cell in soil, enters an extended prepupal stage, and adults emerge in late summer and autumn.



# Siphonaptera

(Fleas)

G. M. DUNNET and D. K. MARDON

Apterous, laterally compressed, endopterygote Neoptera, with piercing and sucking mouth-parts; ectoparasites of mammals and birds. Larvae apodous and vermiform, usually living in nests of hosts. Pupae adecticous, exarate.

This small order of highly specialised insects includes about 2380 described species and subspecies (Lewis and Lewis 1985), 88 described and at least one undescribed species being known to occur in Australia. The adults (Fig. 38.1A) are 1–10 mm long (males usually smaller than females) and strongly sclerotised, and have long legs which enable them to leap characteristically. The body is covered with backwardly directed setae and spines, sometimes arranged in combs (*ctenidia*) facilitating progress through the hair or feathers of the host. Fleas are so modified structurally for their particular kind of parasitic life (Snodgrass 1946) that their relationships with other orders are difficult to determine. They show equally striking biological adaptations, in that all stages, except perhaps the egg, can withstand unfavourable environmental conditions for remarkably long periods. Their phylogeny, classification, host relations, physiology and medical and veterinary importance have been reviewed by Holland (1964) and Traub and Starcke (1980).

## Anatomy of Adult

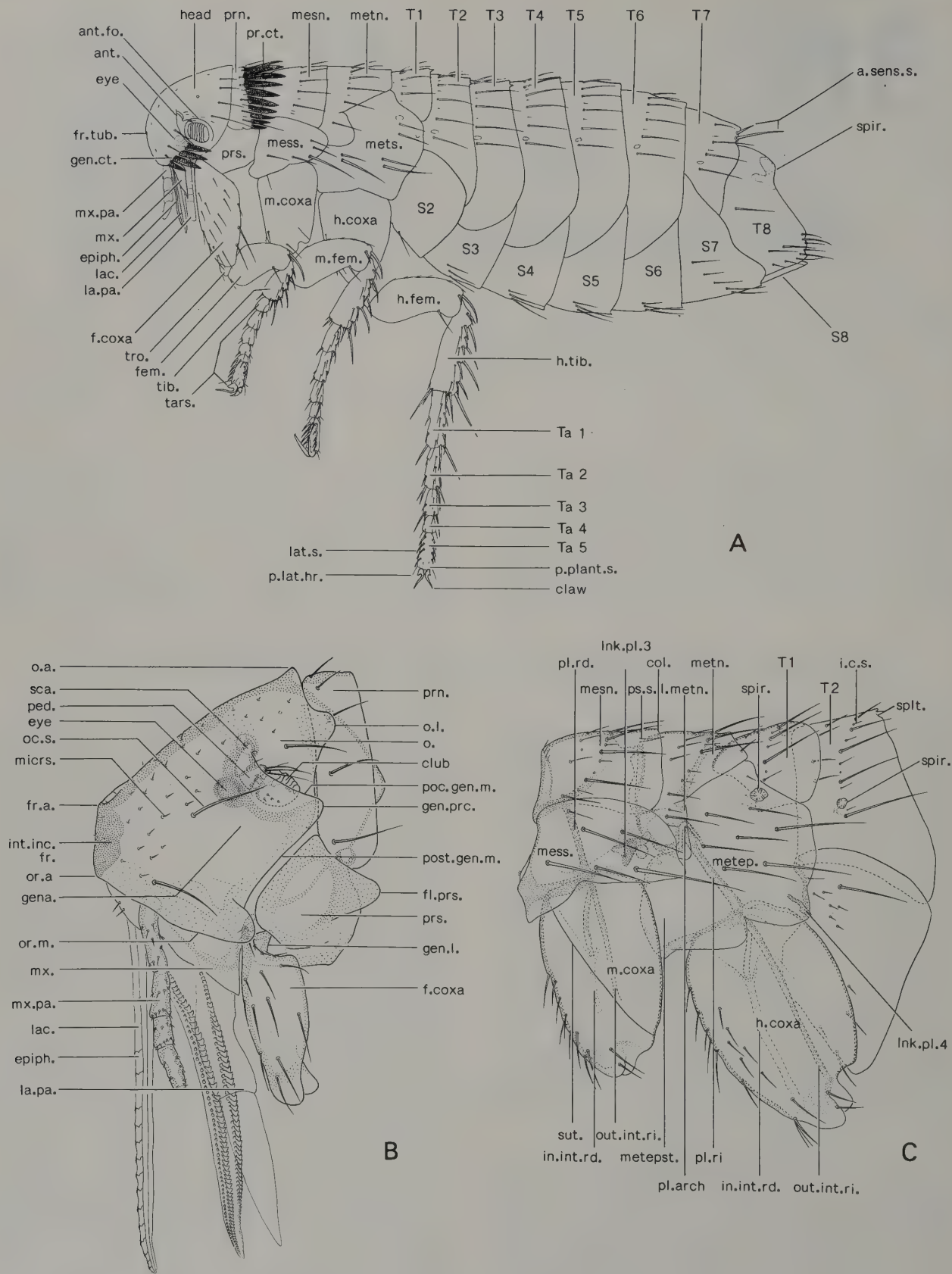
**Head.** Sessile on prothorax; clearly divided laterally by deep antennal groove into frons and occiput. Frons sometimes with small frontal tubercle (Figs 38.4E, 5C, 7F), and sometimes developed into 'helmet' (*Stephanocircus*, Fig. 38.7A). Genal ctenidium may be present (e.g. Figs 38.1A, 4A, D). Compound eyes absent, but atypical lateral ocelli may be large, vestigial or absent. Antennae 3-segmented, with terminal segment usually consisting of 9 units plus a

petiole; lying in a deep groove laterally; usually relatively long in male and used as secondary claspers in copulation. Mouth-parts (Fig. 38.1B) adapted for piercing and sucking; mandibles absent; laciniae of maxillae long, cutting blades more or less serrated on distal portion; stipes short, broad blades; maxillary and labial palps well developed, the latter forming a sheath for the laciniae; epipharynx a long stylet.

**Thorax.** The 3 segments free, prothorax smallest, metathorax largest in association with the strong development of the legs. Prothorax frequently, mesothorax never, and metathorax rarely (in some bat fleas) with a ctenidium. Meso- and metathoracic spiracles present. Arrangement of sclerotised plates and setae is of taxonomic importance.

**Legs.** Long and well developed. Fore legs, especially coxae, modified for pushing through pelage or plumage of hosts; hind legs greatly enlarged for jumping. Articulating surfaces protected by setae. Fifth tarsal segments terminate in a pair of strong claws for clinging to host.

**Abdomen.** Ten segments can be distinguished, the posterior segments, especially in male, considerably modified. Terga with rows of setae and sometimes ctenidia. The dorsal *sensillum* occupies the position of T10, and consists of a number of sensory pits in an elaborate organ protected by a variable number of antesensorial setae on T7. Spiracles on segments 1–8. In the male, S8 may be large, medium-sized, or small, and T8 is contrastingly





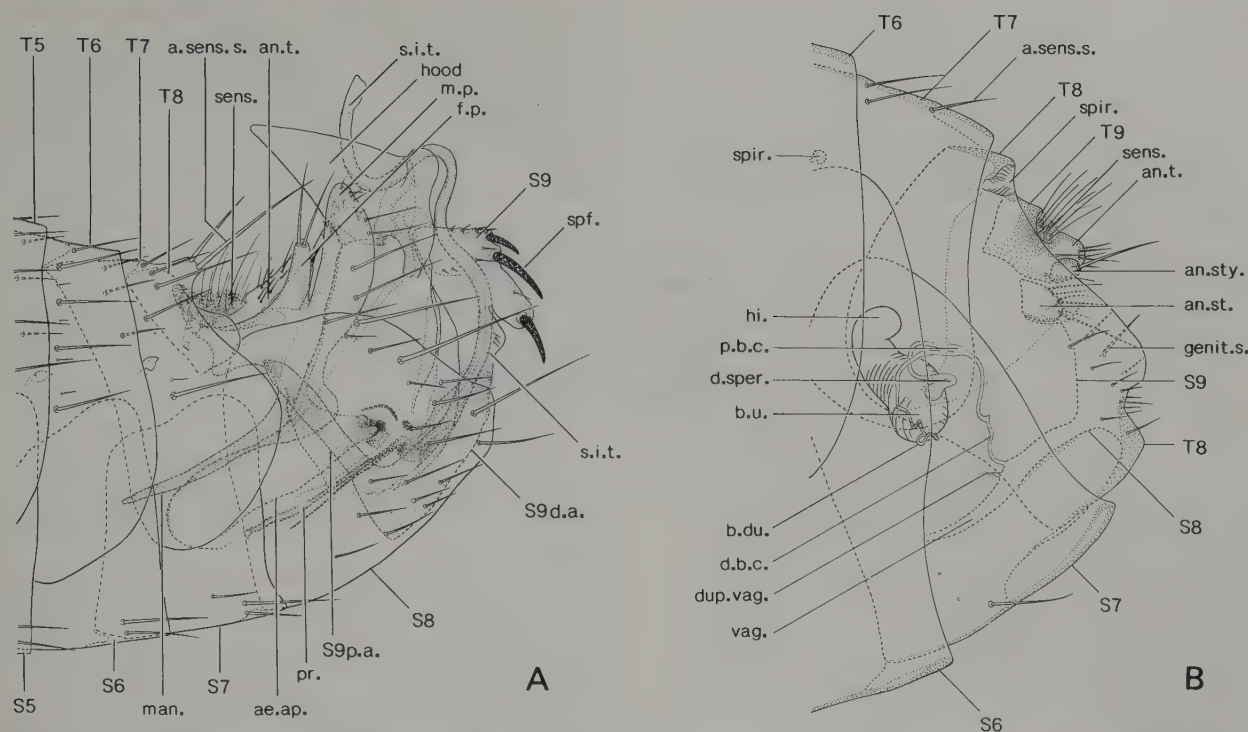


Fig. 38.2 A, *Choristopsylla ochi*, Pygiopsyllidae, ♂: terminal segments 6–10 and genitalia; B, *Echidnophaga octotricha*, Pulicidae, ♀: terminal segments 7–10 and genitalia.

[D. K. Mardon]  
T(5–9), tergum; a. sens. s., antensensillial seta; sens., sensillum; an. t., anal tergum; s. i. t., sclerotised inner tube; m. p., movable process of clasper; f. p., fixed process of clasper; S(5–9), sternum; S9 d.a., sternum 9 distal arm; S9 p.a., sternum 9 proximal arm; p. r., penis rod(s); ae. ap., aedeagal apodeme; man., manubrium; spir., spiracle; hi., hilla of spermatheca; p.b.c., perula of bursa copulatrix; d. sper., duct of spermatheca; b. u., bulga of spermatheca; b. du., blind duct; d. b. c., duct of bursa copulatrix; dup. vag., duplicatura vaginalis; vag., vagina; an. sty., anal stylet; an. st., anal sternum; genit. s., genital seta(e).

small to large; S9 is modified to form an L-shaped clasping organ; and an elaborate clasping organ (T9), consisting of paired manubria and articulating claspers, occupies the posterior tip of the abdomen and encloses the complex aedeagus (e.g. Fig. 38.2A). In the female, the terminal segments are less modified; S7 is frequently shaped and strengthened in a specific way; the spermatheca (paired in Macropsyllidae) is well sclerotised, and its shape and ducts are characteristic features.

**Internal Anatomy.** The principal specialisations are in the digestive tract, in association with feeding on blood. There is a salivary pump for injecting saliva into the wound; cibarial and pharyngeal pumps suck up the blood; the proventriculus is small, and provided with characteristic, radially arranged, sclerotised spines which may act as a valve or as a triturating mechanism; the mid gut is very large. There are 4 Malpighian tubules, and 6 rectal glands. The nervous system is generalised, but with short connectives. The ovaries are panoistic, with few exceptions (not Australian).

Fig. 38.1 A, *Acedestia chera*, Hystrichopsyllidae, ♀: superficial features of left side; B, *Echidnophaga eyrei*, Pulicidae, ♀: head, prothorax, mouth-parts and fore coxa; C, *Choristopsylla ochi*, Pygiopsyllidae, ♀: meso- and metathorax and coxae, abdominal segments 1 and 2.

[D. K. Mardon]  
ant.fo., antennal fossa; ant., antenna; fr. tub., frontal tubercle; gen. ct., genal ctenidium; mx. pa., maxillary palp; mx., maxilla; epiph., epipharynx; lac., lacinia; la. pa., labial palp; f. coxa, fore coxa; tro., trochanter; fem., femur; tib., tibia; tars., tarsus; h. tib., hind tibia; lat. s., lateral setae; p. lat. hr., preapical lateral hairs; p. plant. s., preapical plantar setae; prn., pronotum; pr. ct., pronotal ctenidium; mesn., mesonotum; metn., metanotum; prs., prosternosome; mess., mesosternosome; mets., metasternosome; m. coxa, mid coxa; h. coxa, hind coxa; m. fem., mid femur; h. fem., hind femur; T(1–8), tergum; a. sens. s., antensensillial seta(e); spir., spiracle; S(2–8), sternum; o.a., occipital angle; sca., scape of antenna; ped., pedicel of antenna; micrs., microsetae; fr. a., frontal angle; int. inc. fr., internal incensation of frons; or. a., oral angle; or. m., oral margin; oc.s., ocular seta; o.l., occipital lobe; o., occiput; poc. gen. m., postocular genal margin; gen. prc., genal process; post. gen. m., posterior genal margin; fl. prs., flange of prosternosome; gen. l., genal lobe; pl. rd., pleural rod; lnk. pl. (3, 4), link-plate; ps. s., pseudosetae; col., collar; l. metn., lateral metanotal area; metep., metepimeron; split., spinelet; sut., suture; in. int. rd., inner internal rod; out. int. ri., outer internal ridge; metepst., metepisternum; pl. arch., pleural arch; pl. ri., pleural ridge.

### Immature Stages

**Egg** (Fig. 38.3A). Oval, whitish, often glistening; about 0.5 mm long, and therefore large relative to the size of the adult.

**Larva** (Fig. 38.3B). Vermiform, whitish, rarely parasitic, 4–10 mm long when full-grown. Head usually well developed, with variously serrated mandibles; maxillae small and brush-like; no eyes; antennae 1-segmented. The 13 body segments, each with many stiff setae, are weakly differentiated into thoracic and abdominal; last segment with pair of anal struts.

**Pupa** (Fig. 38.3C). Aedeiticous and exarate, in a thin, loosely constructed cocoon.

### Biology

**Adults.** Both sexes normally live exclusively on blood, but their relationship with their host is not nearly so close as in the case of lice. Larvae are nearly all free living and the adults parasitic only intermittently, even the stickfast fleas (*Echidnophaga*) spending much of their time off the

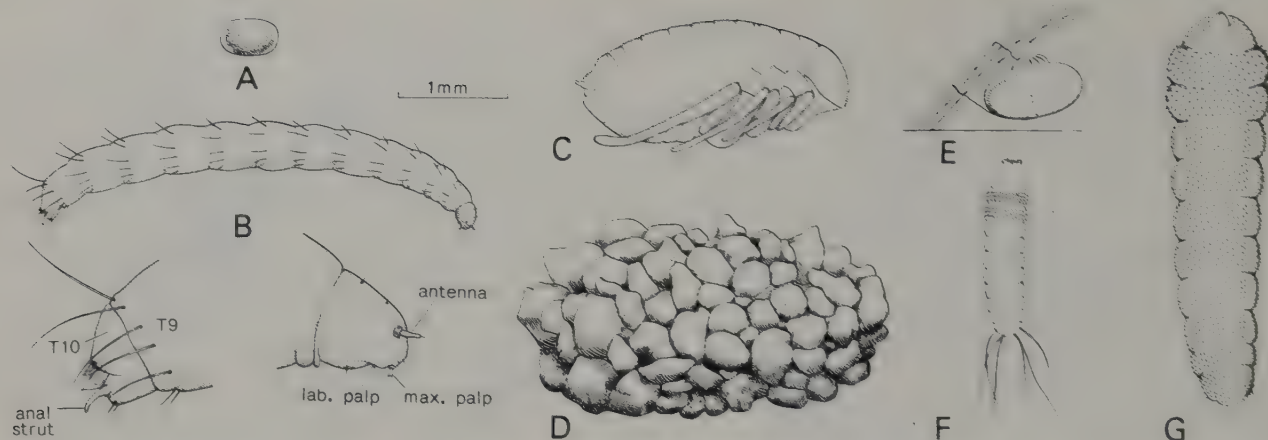


Fig. 38.3 *Ctenocephalides felis*, Pulicidae: A, egg; B, larva, with caudal and cranial ends enlarged; C, pupa; D, sand-encrusted cocoon. Egg and parasitic larvae of *Uropsylla tasmanica*, Pygiopsyllidae, from *Dasyurus* and *Sarcophilus*: E, egg (length 0.65 mm) attached to hair; F, 1st instar larva (body 0.5 mm long); G, full-grown larva (6 mm long) from burrow in skin. [A–D by B. Rankin; E–G by R. M. Warneke]

body of the host. Fleas also quickly leave a dead host and seek a new one, not necessarily of the same species, which accounts for their importance as transmitters of plague. The Pulicoidea are generally more dependent on their hosts than are the Ceratophylloidea and Malacopsylloidea.

The degree of host specificity varies greatly, from the monoxenous *Bradiopsylla echidnae* occurring only on the echidna, to *Echidnophaga myrmecobii* which has 25 known hosts, and *Pygiopsylla hoplia* which is recorded from 35 hosts and occurs regularly on a wide variety of marsupials and rodents and even on domestic livestock. Conversely, whereas some hosts carry only one or two species of flea, others support many (e.g. 22 have been recorded from *Rattus fuscipes* and 11 from *Isoodon obesulus*). Some species are primarily nest fleas, occurring only rarely on the body of the active host, and these usually have a reduced chaetotaxy (e.g. *Acedestia chera* and *Idilla caelebs*). There are relatively few bird fleas (about 132 spp.), all apparently derived from diverse groups that evolved on mammals (Holland 1964). In general, these are nest inhabitants with a life cycle closely linked with the nesting activities of their hosts. Fleas occur on such aquatic mammals as the platypus and *Hydromys*, but not on seals whose ties with the land are brief and often intertidal.

Adults may live for a long time. Thus, Bacot (1914) found that *Pulex irritans* would survive for 125 days unfed and for more than 500 days if fed on humans. *Xenopsylla cheopis* might live for more than a year, and other species for somewhat similar periods, especially in the cocoon, awaiting a stimulus for emergence. These observations explain the not infrequent occurrence of fleas in premises that have been unoccupied for considerable periods. There are few observations on fleas of wild hosts, but Allan (1956) has shown that the European rabbit flea, *Spilopsyllus cuniculi*, may live for over 10 months in association with its host, and there is evidence that species associated with migratory birds overwinter in the nesting places as larvae, pupae and adults.

**Reproduction.** Mating may take place on the host or in

the nest, and may be stimulated simply by warmth or by a blood meal, although a blood meal is usually (perhaps always) necessary for maturation of the ovaries. In *Spilopsyllus cuniculi*, which is highly host-specific, the physiological state of the fleas, their feeding sites, maturation of ova, migration to infant rabbits in the nest, mating and oviposition appear to be governed by the hormone levels, particularly of corticosteroids, in the blood of the host (Mead-Briggs 1977; Rothschild 1965). The breeding cycle of the parasite is thus linked closely with that of the rabbit. This kind of linkage has evident selective advantages for specialised nest breeders; it does not occur in *X. cheopis*, which lives on rats with quite different social and breeding habits from those of the rabbit.

**Life History.** The eggs may be deposited on the body or in the nest of the host. Those deposited on the body are nearly always smooth and soon fall to the ground, whereas those laid in the nest are often sticky and adhere to the substrate. They are usually laid a few at a time, and *P. irritans* may lay a total of more than 400 in the course of its life (Bacot 1914). The incubation period of the egg usually varies from about 2 to 12 days, and the 1st instar larva frees itself from the shell by means of a sharp egg-burster (or egg-tooth) on its head. The immature stages of most species studied require moderately high temperatures (20–30°C) and humidities (70% or more) for development, but the larvae of the domesticated species, which often live in dust on floors and similar situations, may be able to resist adverse conditions better than those that are restricted to nests. Duration of the (usually 3) larval instars varies from about 10–15 days to over 200, depending on the conditions to which they are exposed, and the pupa may require similar periods before emergence. In laboratory cultures, Sharif (1937) reported total developmental periods of 25–65 days for *Nosopsyllus fasciatus* and Kerr (1946) 20–24 days for *Ctenocephalides felis*.

Flea larvae have occasionally been found on the bodies of their hosts, but the only species with truly parasitic larvae would appear to be *Uropsylla tasmanica* which lives on dasyurids in Tas. and Vic. (Warneke unpubl.). In this species the eggs (Fig. 38.3E) are cemented to the fur



of the host, and the 1st instar larvae (Fig. 38.3f) have large mandibles which are used for tearing the chorion and penetrating the skin. Older larvae (Fig. 38.3g) are considerably modified, with very small heads, considerably expanded second and third trunk segments, specialised spines on the body, and probably only the 3 posterior pairs of spiracles functional. They live in burrows extending into the dermis, with only the posterior segments protruding, quickly withdrawing them into the burrow if disturbed. When mature, they drop to the ground, and spin a cocoon in the normal way.

**Natural Enemies.** No enemies of fleas, other than their hosts, have been recorded in Australia.

**Economic Significance.** The human (*Pulex irritans*), cat (*Ctenocephalides felis*) and dog (*Ct. canis*) fleas can be serious domestic pests, because many people become sensitised to their bites. Much more significant in terms of public health is their role as transmitters of disease from mammalian hosts to humans: especially plague, from rodents, where the oriental rat flea *Xenopsylla cheopis* is most frequently implicated; and also murine typhus (*Rickettsia*) and tularemia (*Francisella*). Australia has been substantially free of bubonic plague with only occasional outbreaks at seaports, and none recently; sylvatic plague is unknown here. The less dangerous disease, murine typhus, is endemic in country towns. Tularemia is not known in Australia.

Fleas also serve as intermediate hosts of the dog tapeworm, *Dipylidium caninum*, and the rodent tapeworm, *Hymenolepis diminuta*, both of which occasionally infect children, of one of the dog filarioids, *Dipetalonema reconditum*, and of the non-pathogenic protozoan *Trypanosoma lewisi* of rats. All these parasites have been recorded in Australia.

It was thought that species of *Echidnophaga*, stickfast fleas occurring naturally in Australia, and parasitising rabbits, might be useful in spreading myxomatosis among rabbits here, but Fenner and Ratcliffe (1965) found that they did not contribute to epizootics in the field. However, the European rabbit flea *Spilopsyllus cuniculi* was first introduced to Australia in 1966, and released in a number of geographical and climatic areas. It became established and spread, and now plays a role in bringing about outbreaks of myxomatosis in rabbit populations at least in Vic. (Shepherd 1980).

The veterinary importance of fleas in Australia was reviewed by Roberts (1952).

### Special Features of the Australian Fauna

The Australian flea fauna, monographed by Dunnet and Mardon (1974), exhibits a high degree of endemism, like the mammals with which most are associated. Of the 88

species and subspecies now recognised as Australian, 10 are thought to have been introduced by humans, most of them now cosmopolitan due to their association with humans or domestic or commensal animals. Of the remaining 78 indigenous forms, 67 (86%) are endemic. Of the 11 indigenous but not endemic species, 2 were introduced to New Zealand from Australia, 4 are on Macquarie I. and other subantarctic islands, 2 are also present in New Guinea but nowhere else, while one occurs on bats also in Java and the Philippines, and one on rats also in New Guinea, the Philippines, Hawaii, Vietnam and Thailand. One species is recorded also from India. The endemic fauna includes members of 7 of the 9 families represented in Australia.

The dominant family is the Pygiopsyllidae, with 41 species and subspecies in Australia, of which all but 6 are endemic. Three subfamilies are recognised, Lycopsyllinae (8 spp.) confined to Australia; Pygiopsyllinae (30 Australian spp., 26 non-Australian spp.) centred in Australia and New Guinea but with representatives in New Zealand, subantarctic islands, Borneo and South America (1 genus); and Stivaliinae (3 Australian spp., 116 non-Australian spp. and subsp.) centred in New Guinea, with a monophyletic group of genera centred in South-East Asia and reaching eastern Asia, India and Africa.

Stephanocircidae are known only from Australia and South America, with a distinct subfamily on each continent. The Stephanocircinae includes 9 spp. and subsp. endemic to Australia, the Craneopsyllinae 30 spp. and subsp. endemic in South and Central America. The Macropsyllidae, with two monotypic genera, are confined to Australia.

The family Pulicidae is represented by 19 species and subspecies, of which 11 are endemic, another 2 are probably indigenous, and the remaining 6 are introduced.

The Hystrihopsyllidae, subfamily Doratopsyllinae, is represented in Australia by 2 monotypic genera comprising an endemic tribe Acedestiini, a puzzling zoogeographical link (Mardon 1978b).

The Ischnopsyllidae, bat fleas, occur world-wide, but of the 7 species (4 genera) known in Australia, 6 species and 2 genera are endemic.

The Rhopalopsyllidae, with 4 species (2 endemic) on Australian seabirds, is a predominantly Neotropical family associated with rodents, but one genus occurs on seabirds throughout the Southern Ocean.

The Australian fauna is markedly distinct, but with strong links with New Guinea. Outside Australia and New Guinea, the strongest links are with the Neotropical Region both in geological time scales (Stephanocircidae, Pygiopsyllidae) and more recent (Rhopalopsyllidae, Pygiopsyllidae).

## CLASSIFICATION

### Order SIPHONAPTERA (88 Australian spp. and subsp.)

#### PULICOIDEA (19)

##### Tungidae (0)

##### 1. Pulicidae (19)

#### MALACOPSYLLOIDEA (4)

##### 2. Rhopalopsyllidae (4)

##### Malacopsyllidae (0)

#### CERATOPHYLLOIDEA (65)

##### Vermipsyllidae (0)

##### 3. Hystrihopsyllidae (2)

- Coptosyllidae (0)  
 4. Pygiopsyllidae (41)  
 5. Stephanocircidae (9)

6. Macropsyllidae (2)  
 Xyphiopsyllidae (0)  
 Ancistropsyllidae (0)  
 Chimaeropsyllidae (0)

7. Ischnopsyllidae (7)  
 8. Leptopsyllidae (1)  
 9. Ceratophyllidae (3)

Holland's (1964) statement that the classification of the Siphonaptera is 'scarcely ripe for stable conclusions' still applies. There is as yet no generally accepted classification within the order, with several classifications published in recent years having significantly different treatments of Australian family-group taxa (e.g. Lewis 1972–75; Lewis and Lewis 1985; Mardon 1978a; Smit 1982, 1983). The 3 superfamilies are distinguished by combinations of characters, some of which occur in more than one.

Some workers give no reasoned explanation of their classification, and sometimes omit to list subordinate taxa included (e.g. Smit 1973, 1979, 1982) while in other cases an explanation of methods and criteria is given (e.g. Mardon 1978a, b). The classification followed here is that of Hopkins and Rothschild (1962, 1966) and Mardon (1981). Australian taxa are treated significantly differently by Smit (1982).

#### Key to the Genera of Siphonaptera Known in Australia

1. Abdominal terga 2–7 (T2–7) with only 1 row of setae ..... 2  
 Abdominal terga 2–7 (T2–7) with more than 1 row of setae (though anterior row may be reduced, e.g. in Ischnopsyllidae) ..... 9
- 2(1). Pronotal and genal ctenidia present ..... 3  
 Pronotal and genal ctenidia absent ..... 6
- 3(2). Frons without internal incassation (e.g. Figs 38.4B, C); pronotum dorsally less than half the length of its dorsal spines; 4 sharp genal spines ..... 4  
 Frons with conspicuous, more or less club-shaped, internal incassation (Figs 38.4A, D); pronotum dorsally more than half length of its dorsal spines; genal spines usually more than 4; if 4, then blunt, not pointed ..... 5
- 4(3). Integricipit (without well developed interantennal suture) (Figs 38.1A, B); pleural arch (Fig. 38.1C) present; all 4 pairs of plantar setae on hind tarsal segment 5 lateral ..... *Acedestia* (Hystrichopsyllidae)  
 Fracticipit (with well developed interantennal suture) (Figs 38.7B, C, E); pleural arch absent; hind tarsal segment 5 with 3 pairs of lateral plantar setae and 1 pair on plantar surface between basal lateral pair (Fig. 38.1A) ..... *Idilla* (Hystrichopsyllidae)
- 5(3). Genal ctenidium horizontal, of curved sharp spines; genal process with small sharp spine; frontal tubercle absent (Fig. 38.4D) ..... *Ctenocephalides* (Pulicidae)  
 Genal ctenidium near vertical, of straight blunt spines; genal process without spine; small frontal tubercle present (Fig. 38.4A) ..... *Spilopsyllus* (Pulicidae)
- 6(2). Frons angulate and more or less heavily sclerotised (e.g. Fig. 38.1B); thoracic segments reduced, metanotum dorsally much shorter than half length of abdominal T1 ..... *Echidnophaga* (Pulicidae)  
 Frons rounded and not heavily sclerotised; thoracic segments not so reduced, metanotum dorsally as long as or longer than half length of T1 ..... 7

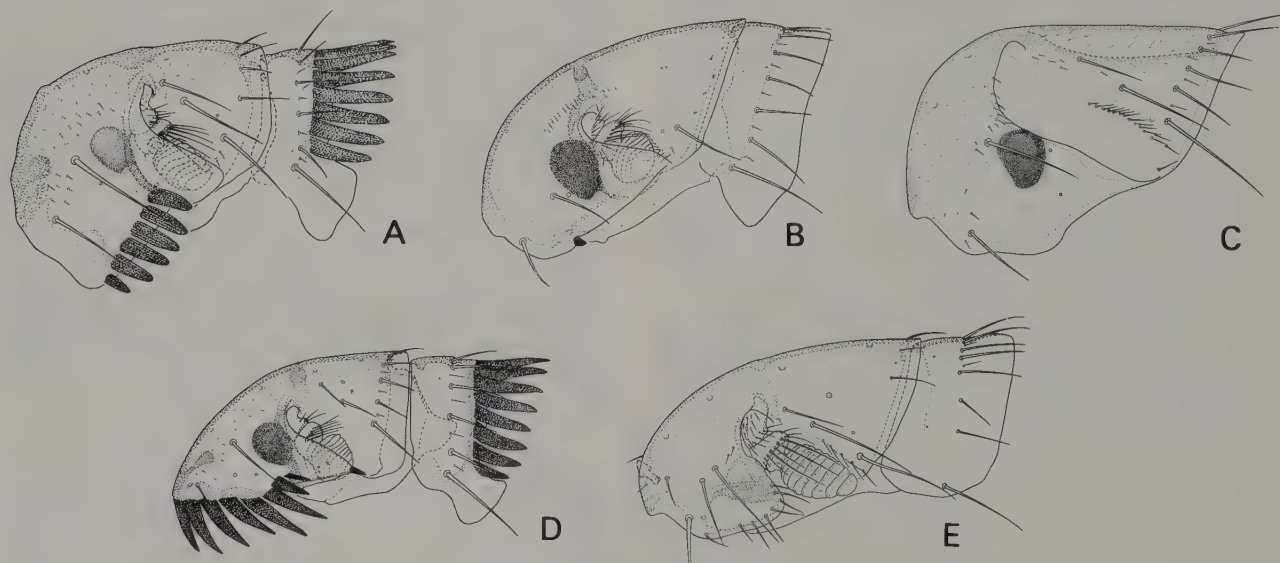


Fig. 38.4 A, *Spilopsyllus cuniculi*, Pulicidae, ♀: head and pronotum; B, *Pulex irritans*, Pulicidae, ♂: head and pronotum; C, *Xenopsylla vexabilis*, Pulicidae, ♂: head (antenna omitted); D, *Ctenocephalides felis*, Pulicidae, ♀: head and pronotum; E, *Parapsyllus australiacus*, Rhopalopsyllidae, ♀: head and pronotum.

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- 7(6). Downward-pointing frontal tubercle present (Fig. 38.5c); outer internal ridge of mid coxa (Fig. 38.1c) present; fourth link-plate (Fig. 38.1c) present; antensensilial setae absent. [On wombats] ..... *Lycopsylla* (Pygiopsyllidae)  
 Frontal tubercle absent (Figs 38.4b, c); outer internal ridge of mid coxa absent; fourth link-plate absent; antensensilial setae present ..... 8
- 8(7). Pleural rod of mesothorax (Fig. 38.1c) present; genal margin without spine; interantennal ridge absent; postantennal head with about 6–8 large setae (Fig. 38.4c). [On rats] ..... *Xenopsylla* (Pulicidae)  
 Pleural rod of mesothorax absent; genal margin with small spine below eye; interantennal ridge present; postantennal head with only one large seta each side (Fig. 38.4b) ..... *Pulex* (Pulicidae)
- 9(1). Pronotum without conspicuous, well-developed ctenidium; at most a small, dorsal ctenidium of 2–3 spines each side, in which case there is a postocular spine ..... 10  
 Pronotum with conspicuous, well-developed ctenidium ..... 12
- 10(9). Frons with arrow-shaped, upward-pointing, recessed tubercle (Fig. 38.4e); one antensensilial seta each side; no terga with marginal spinelets. [On seabirds, in their nests, or on rats in seabird colonies] ..... *Parapsyllus* (Rhopalopsyllidae)  
 Frontal tubercle absent; 2 antensensilial setae each side; some terga with marginal spinelets ..... 11
- 11(10). Eye with postocular spine and no ventral sinus (Fig. 38.5a); pronotum with small dorsal ctenidium of 2–3 spines each side; metanotum with several rows of short spiniform setae; nota and terga with posterior rows of very large setae. [On echidna] ..... *Bradiopsylla* (Pygiopsyllidae)  
 Eye with no postocular spine but with obvious ventral sinus (Fig. 38.6d); pronotum without spines; metanotum with several rows of fine setae; nota and terga with posterior rows of relatively small setae. [On seabirds] ..... *Notiopsylla* (Pygiopsyllidae)
- 12(9). Genal ctenidium absent ..... 13  
 Genal ctenidium present ..... 24
- 13(12). Antensensilial setae absent; pronotum exceptionally deep, more than twice as long dorsally as laterally with a long ctenidium of 14–16 sharp spines each side (Fig. 38.5d); metanotum and T1–6 with prominent marginal spinelets ..... *Uropsylla* (Pygiopsyllidae)  
 Antensensilial setae present; pronotum at most only barely longer dorsally than laterally, its ctenidium usually with not more than 12 spines each side; if more than 12 then either frontal tubercle present or hind tibia with 6 dorsoposterior notches ..... 14
- 14(13). Small downward-pointing frontal tubercle present (Fig. 38.7f); sensillum flat; fourth link-plate absent; metanotum with marginal spinelets ..... 15  
 Frontal tubercle absent; sensillum more or less convex; fourth link-plate present (Fig. 38.1c) (not always clearly visible); metanotum without marginal spinelets ..... 16
- 15(14). Pronotal ctenidium of at least 12 spines each side; eye large; S8 of ♂ conspicuous with prominent apical setae; bulga of spermatheca not spherical ..... *Ceratophyllus* (Ceratophyllidae)  
 Pronotal ctenidium of fewer than 12 spines each side; eye smaller; S8 of ♂ reduced, almost absent; bulga of spermatheca roughly spherical ..... *Nosopsyllus* (Ceratophyllidae)
- 16(14). Pronotal spines narrow, about 14–15 each side; hind tibia with 6 dorsoposterior notches bearing stout setae; tarsal segment 5 with one median pair of setae displaced well onto plantar surface and 3 preapical plantar setae ..... *Geohollandia* (Pygiopsyllidae)  
 Pronotal spines not more than 12 each side; hind tibia with more than 6 distinct dorsoposterior notches bearing stout setae; tarsal segment 5 not as above ..... 17
- 17(16). Pronotum with only one row of setae (Fig. 38.5b); prosternosome (the entire pleurosternal plate of the prothorax) with posterior ventral projection; tarsal segment 5 with 4 pairs of lateral setae and one pair on plantar surface between basal lateral pair ..... *Choristopsylla* (Pygiopsyllidae)  
 Pronotum with more than one row of setae; prosternosome without posterior ventral projection; tarsal segment 5 not as above, except in *Austropsylla* (see couplet 18) ..... 18
- 18(17). Pronotal ctenidium reduced in size, confined to dorsal two-thirds of posterior notal margin, but with about 10 spines each side; false ctenidia on S3–6; tarsal segment 5 with a pair of plantar setae almost between but slightly proximal of basal lateral pair ..... *Austropsylla* (Pygiopsyllidae)  
 Pronotal ctenidium not so reduced, extending down whole of posterior notal margin; sterna without false ctenidia; tarsal segment 5 with the basal pair of plantar setae lateral or with first and third pairs displaced onto plantar surface ..... 19
- 19(18). Frons with 1–4 short spiniform setae in anterior row (e.g. Fig. 38.6b), well differentiated from other head setae which are all slender and unmodified; outer surface of hind tibia with 2 longitudinal rows of setae, median and posterior, plus a few anterior submarginal ones; setae of posterior tergal row many times as large as those of other rows ..... *Acanthopsylla* (Pygiopsyllidae)  
 Frons without such spiniforms in anterior row, setae on the head either all more or less slender (e.g. Fig. 38.6c) or mostly stout (e.g. Fig. 38.6e); outer surface of hind tibia with clearly more than 2 longitudinal rows of setae, or if only 2 rows then tergal setae of anterior rows about half the size of those of posterior rows ..... 20
- 20(19). Setae on head mostly stout (Fig. 38.6e); eye (Fig. 38.6e) overlapping ventral postgenal margin; pronotum shorter than its dorsal spines (Fig. 38.6e); either T7 with a distinct dorsal lobe projecting caudad between the pairs of antensensilial setae, or pronotal spines sharply acuminate apically ..... 21

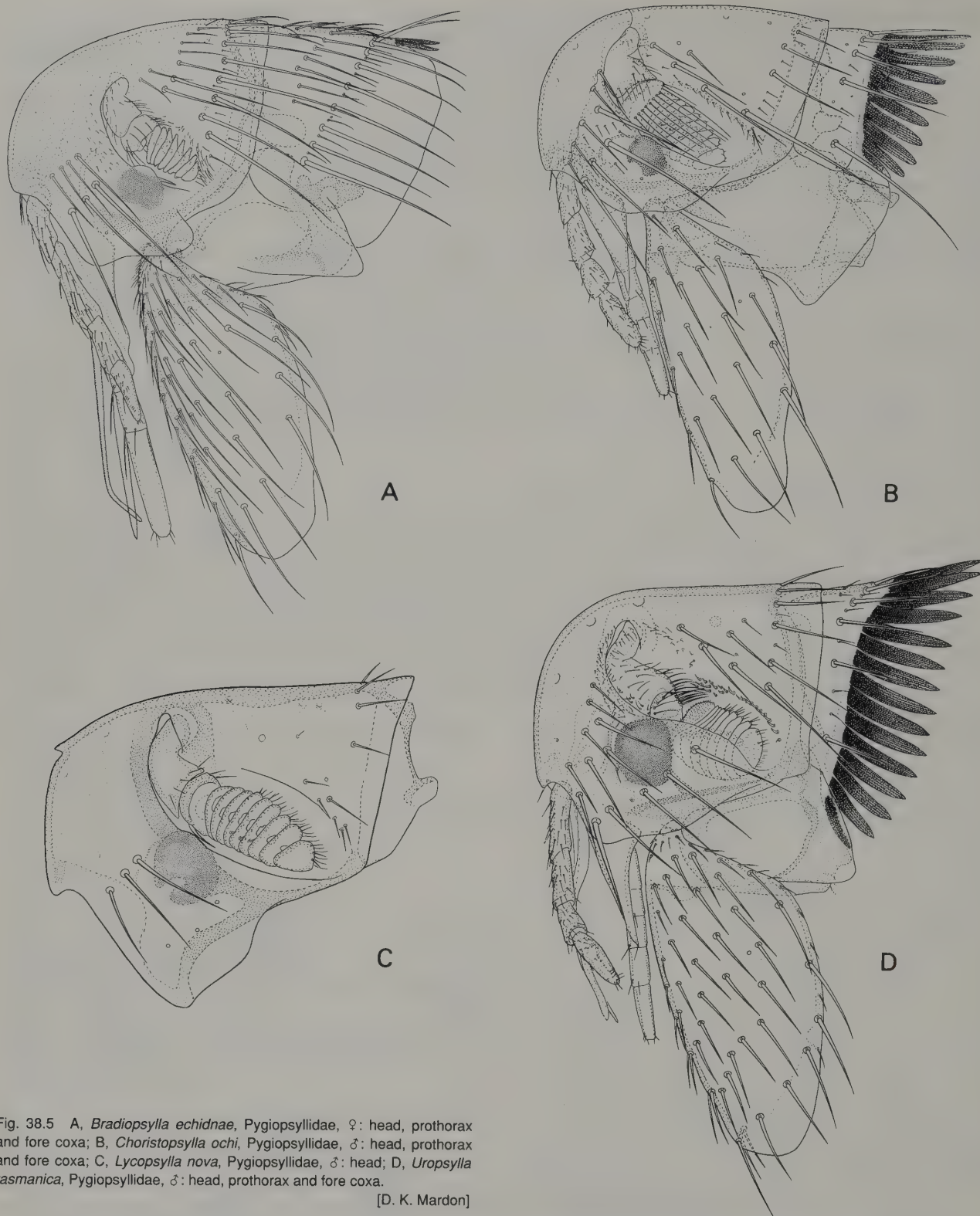


Fig. 38.5 A, *Bradiopsylla echidnae*, Pygiopsyllidae, ♀: head, prothorax and fore coxa; B, *Choristopsylla ochi*, Pygiopsyllidae, ♂: head, prothorax and fore coxa; C, *Lycopsylla nova*, Pygiopsyllidae, ♂: head; D, *Uropsylla tasmanica*, Pygiopsyllidae, ♂: head, prothorax and fore coxa.

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- Setae on head not generally stout (Fig. 38.6C); eye clearly dorsad of postgenal margin (Fig. 38.6C); pronotum about as long as or longer than its dorsal spines (Fig. 38.6C); T7 without a pronounced lobe between the pairs of antesensilial setae; pronotal spines not sharply acuminate apically ..... 22
- 21(20). Setae of anterior frontal row subspiniiform (Fig. 38.6E); pronotal spines distinctly longer than the notum dorsally and blunt apically (Fig. 38.6E); mouth-parts short, 5-segmented labial palp reaches to about two-thirds length of fore coxa ..... *Metastivalius* (Pygiopsyllidae)



- Setae of anterior frontal row not subspiniiform; pronotal spines slightly longer than the notum dorsally, becoming progressively shorter ventrally, and sharply acuminate apically; mouth-parts longer, 6-segmented labial palp reaches to apex of fore coxa ..... *Parastivalius* (Pygiopsyllidae)
- 22(20). Setae of posterior tergal row less than twice the size of those of the anterior 2 rows; outer surface of hind tibia with only about 2 longitudinal rows of setae; tarsal segment 5 with the first and third pairs of strong plantar setae displaced well onto plantar surface ..... *Wurunjerria* (Pygiopsyllidae)
- Setae of posterior tergal row more than twice the size of those of the anterior rows; outer surface of hind tibia with clearly more than 2 longitudinal rows of setae; tarsal segment 5 with the strong plantar setae all lateral ..... 23
- 23(22). Hind tibia with 7 notches bearing stout setae in dorsoposterior margin; second segment of maxillary palp at most one-fourth longer than first; smaller, less strongly setose species ..... *Pygiopsylla* (Pygiopsyllidae)
- Hind tibia with 8 notches bearing stout setae in dorsoposterior margin; second segment of maxillary palp at least half as long again as first; larger, more strongly setose species ..... *Bibikovana* (Pygiopsyllidae)
- 24(12). Occiput with a conspicuous, single, internal tubercle (e.g. Fig. 38.7A) ..... 25
- Occiput without a conspicuous, single, internal tubercle (e.g. Figs 38.7D, E) ..... 28
- 25(24). Head with vertical anterior helmet with a conspicuous ctenidium, and a separate vertical genal ctenidium (e.g. Fig. 38.7A) ..... 26
- Head without vertical anterior helmet, but with an angled genal ctenidium extending up the anterior margin of antennal fossa (e.g. Fig. 38.7B) ..... 27
- 26(25). Complete ctenidium on T1; fore and mid tibia each with a longitudinal false ctenidium ..... *Coronapsylla* (Stephanocircidae)

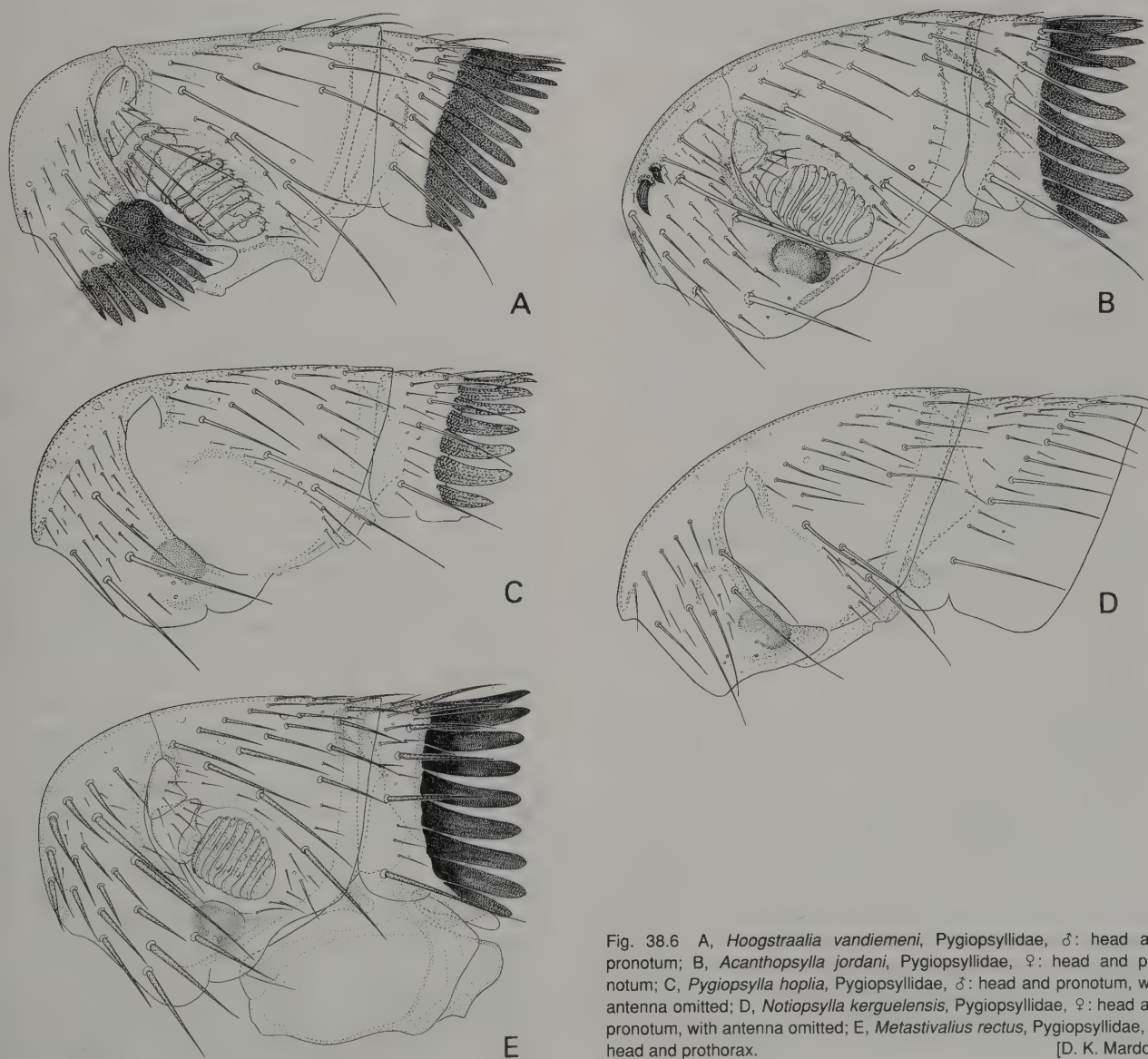


Fig. 38.6 A, *Hoogstraalia vandiemeni*, Pygiopsyllidae, ♂: head and pronotum; B, *Acanthopsylla jordani*, Pygiopsyllidae, ♀: head and pronotum; C, *Pygiopsylla hoplia*, Pygiopsyllidae, ♂: head and pronotum, with antenna omitted; D, *Notiopsylla kerguelensis*, Pygiopsyllidae, ♀: head and pronotum, with antenna omitted; E, *Metastivalius rectus*, Pygiopsyllidae, ♀: head and prothorax. [D. K. Mardon]

- Ctenidium on T1 reduced or absent; fore and mid tibiae without longitudinal false ctenidia (Fig. 38.7A) ..... *Stephanocircus* (Stephanocircidae)
- 27(25). Frons strongly convex, its anterior margin steeply inclined (Fig. 38.7B); long ctenidia on T2–5 or 6 ..... *Macropsylla* (Macropsyllidae)
- Frons not strongly convex, its margin nowhere steeply inclined; short ctenidia on T1–4 ..... *Stephanopsylla* (Macropsyllidae)
- 28(24). Genal ctenidium post-oral, of more than 2 spines ..... 29
- Genal ctenidium pre-oral, of 2 spines. [On bats] ..... 30
- 29(28). Frons with submarginal spiniforms at angle; genal ctenidium of 4 blunt spines (Fig. 38.7E) ..... *Leptopsylla* (Leptopsyllidae)
- Frons with neither spiniforms nor angle; genal ctenidium of 8–12 pointed spines (Fig. 38.6A) ..... *Hoogstraalia* (Pygiopsyllidae)
- 30(28). Metanotum and abdominal terga without ctenidia, at most with marginal spinelets, and mostly with a conspicuous tuberculiform incrassation; frons with either a dark band or a pale band, but not both ..... 31
- Metanotum and some abdominal terga each with a ctenidium and without a tuberculiform incrassation; frons with pale band bounded posteriorly by a dark, striated band (e.g. Fig. 38.7D) ..... 32
- 31(30). Frons with pale band on either side of anterior row of setae, with no dark striated band; dorsal wall of occiput with several distinct tuberculiform incrassations ..... *Lagaropsylla* (Ischnopsyllidae)
- Frons with no pale band, but with dark striated band anterad of front row of setae (Fig. 38.7C); dorsal wall of occiput without tuberculiform incrassations ..... *Coorilla* (Ischnopsyllidae)
- 32(30). Dorsal apex of preantennal part of head with a small laterally projecting lobe just overlapping the interantennal suture; pronotum short, distinctly shorter than its spines ..... *Serendipsylla* (Ischnopsyllidae)
- Dorsal apex of preantennal part of head with no such lobe, with simple margin (Fig. 38.7D); pronotum longer, longer than its spines (Fig. 38.7D) ..... *Porribius* (Ischnopsyllidae)

### Superfamily PULICOIDEA

**1. Pulicidae.** This family is world-wide and is represented in Australia by 5 genera and 18 species. Five species are cosmopolitan, associated with humans and their domestic or commensal animals (e.g. cat, dog, rat and human fleas), and one, *Spilopsyllus cuniculi*, the European rabbit flea, was deliberately introduced as a potential vector of myxomatosis. Only 12 species belonging to two genera *Xenopsylla* and *Echidnophaga* are indigenous. *Xenopsylla* spp. occur on native rats. *Echidnophaga* spp. occur on a wide range of hosts; 4 are especially associated with the 3 species of wombats.

### Superfamily MALACOPSYLLOIDEA

**2. Rhopalopsyllidae.** This family has 12 genera, of which all but one, *Parapsyllus*, are Neotropical in distribution, mostly associated with rodents and other mammals. *Parapsyllus* has become associated with seabirds (especially penguins and petrels) and the genus has now diversified into many species, especially in the New Zealand subantarctic islands where they also infest ground-nesting parakeets. In Australia 2 species occur round the southern coast, and two others are known from Macquarie I.

### Superfamily CERATOPHYLLOIDEA

**3. Hystrichopsyllidae.** This large family is represented by only 2 specialised endemic genera constituting the tribe Acedestiini, of the subfamily DORATOPSYLLINAE. *Acedestia* is monotypic, and *A. chera* is only rarely collected from bandicoots and potoroos in southern Australia. *Idilla* is also monotypic; *I. caelebs* is rarely collected, and believed to be a 'nest flea' on *Antechinus flavipes*, recorded only in N.S.W.

**4. Pygiopsyllidae.** This family has 13 genera and over

40 species in Australia with many other species in New Guinea and South-East Asia, and one endemic genus in South America.

*Lycopsylla* is an endemic genus of 2 species, each monoxenous on the commoner 2 species of wombat in south-eastern Australia. *Uropsylla* is an endemic, monotypic genus. *U. tasmanica* parasitises the larger dasyurids, and has an unusual life cycle including a parasitic larva which burrows into the skin of its host. *Bradiopsylla* is also endemic and monotypic, with *B. echidnae* parasitic on echidnas in south-eastern Australia. *Choristopsylla* is an endemic genus with 4 species associated with arboreal marsupials of the families Phalangeridae, Petauridae and Burramyidae. The above 4 genera are regarded by Mardon (1978a) as constituting the subfamily LYCOPSYLLINAE, each in a monotypic tribe. The subfamily PYGIOPSYLLINAE includes the following 7 genera. Of the 6 species of *Pygiopsylla*, 5 are indigenous in Australia. They are associated mainly with marsupials and rodents. *P. hoplia*, the most commonly recorded Australian flea, and the similar *P. phiola*, have been introduced to New Zealand. *Bibikovana* is a mainly Australian genus of 13 species and subspecies: 7 species are endemic in Australia, associated with both marsupials and rodents; 4 are endemic in New Guinea and appear to be derived from a common Australian ancestor but *B. tiptoni* in Borneo is closely related to the Australian *B. rainbowi*. *Notiopsylla* is a subantarctic genus associated with seabirds and centred on the New Zealand subregion, with 2 species-group taxa on Macquarie I. but not yet recorded in Tas. *Geohollandia* is monotypic; *G. solida*, with but a single Australian record, is known from bird nests in New Guinea, and has morphological characters typical of bird fleas. *Wurunjerria* is also monotypic and endemic; *W. warnekei* is known only from the arboreal *Gymnobelideus*



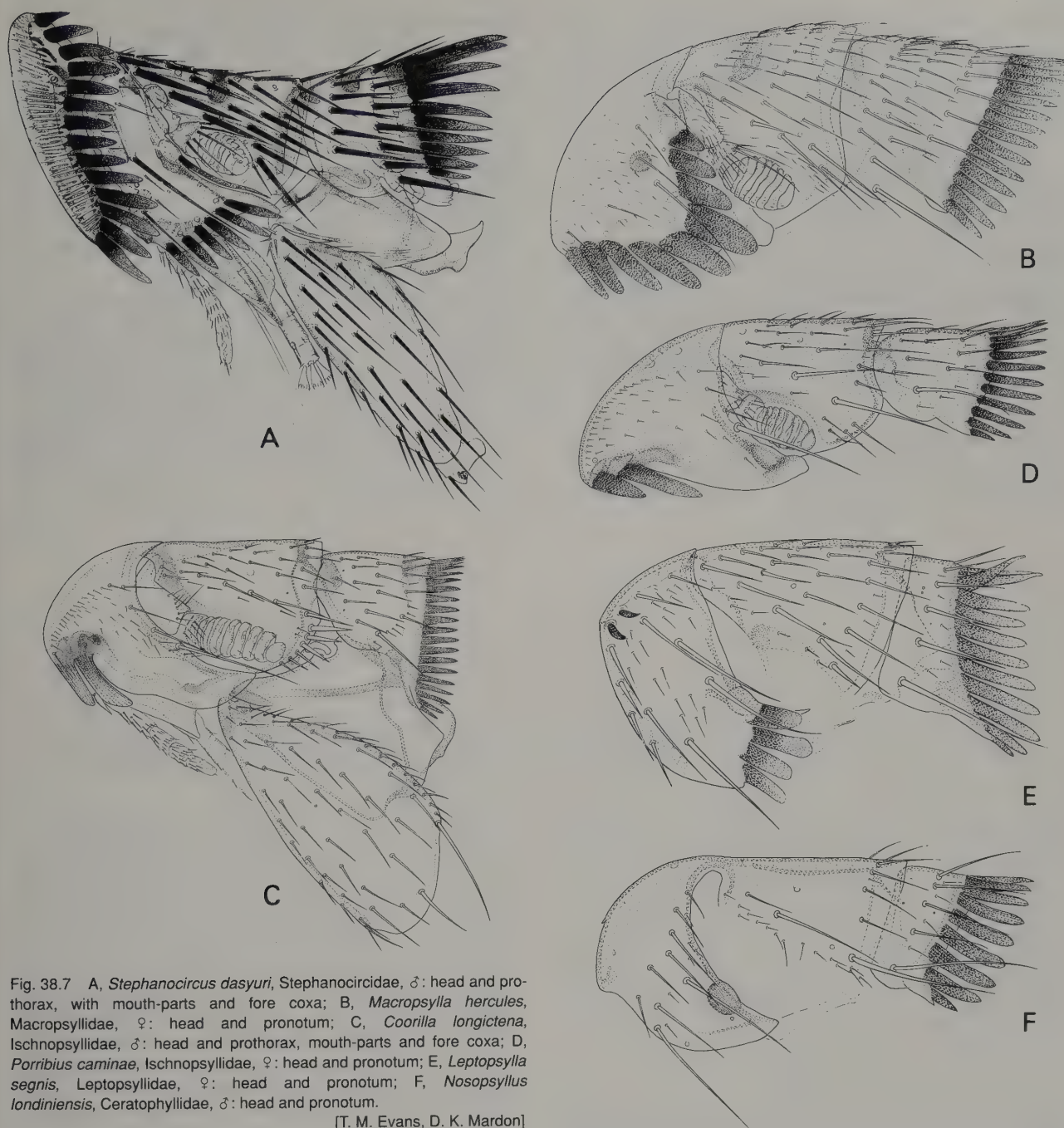


Fig. 38.7 A, *Stephanocircus dasyuri*, Stephanocircidae, ♂: head and prothorax, with mouth-parts and fore coxa; B, *Macropsylla hercules*, Macropsyllidae, ♀: head and pronotum; C, *Coorilla longictena*, Ischnopsyllidae, ♂: head and prothorax, mouth-parts and fore coxa; D, *Porribius caminae*, Ischnopsyllidae, ♀: head and pronotum; E, *Leptopsylla segnis*, Leptopsyllidae, ♀: head and pronotum; F, *Nosopsyllus londiniensis*, Ceratophyllidae, ♂: head and pronotum.

[T. M. Evans, D. K. Mardon]

*leadbeateri* in Vic. The genus *Acanthopsylla* occurs in both Australia and New Guinea, with 19 species and sub-species of which 12 are Australian, mainly associated with marsupials, and also rodents. *Hoogstraalia* is a genus of bird fleas, with 4 species, each respectively in the Philippines, New Guinea, Australia and New Zealand; the Australian species *H. vandiemeni* is known only from Tas. The subfamily STIVALIINAE is represented in Australia by 2 genera. *Metastivalius* is a predominantly New Guinean genus with 9 described species and several known but yet undescribed; the Australian species *M. rectus* and *M. molestus* are known only from rats in Qld. *Parastivalius* is also a New Guinean genus with 5

species; its sole Australian species *P. novaeguineae*, also occurs in New Guinea, associated with bandicoots.

**5. Stephanocircidae.** The 9 species of stephanocircids, in 2 genera, are the spectacular helmet-fleas of Australia, so-called because of a striking modification of the head (Fig. 38.7A). The Australian representatives are in the endemic subfamily STEPHANOCIRCINAE, while there is also an endemic South American subfamily, Craneopsyllinae. *Stephanocircus* species and subspecies occur on a variety of marsupial and rodent hosts. *Coronapsylla* is close to *Stephanocircus*, and monotypic; *C. jarvisi* is known from *Antechinus* spp. in south-eastern Australia.

**6. Macropsyllidae.** An endemic family with 2 dis-

inctive monotypic genera. *Macropsylla hercules* is one of the most recognisable and largest Australian fleas, widely recorded in south-eastern Australia, mainly from rats. *Stephanopsylla thomasi* shares some unusual characters with *Macropsylla*, but there are only a few widely separated records from marsupials in Vic. and W.A.

**7. Ischnopsyllidae.** A world-wide family of fleas parasitising bats. There are 4 genera in Australia. *Porribius* has 4 species, 2 of which are endemic Australian, both widely distributed on various microchiropteran hosts. *Coorilla* is endemic with 3 species, all from molossid bats in eastern Australia. *Lagaropsylla* has 18 species, distributed in the Ethiopian, Oriental and Australian regions; one species, *L. mera*, occurs in Australia, and also in Indonesia and the Philippines. *Serendipsylla* is endemic and monotypic, with *S. marshalli* described from *Macroderma gigas*.

**8. Leptopsyllidae.** A widespread, modern, Northern Hemisphere family, represented in Australia only by an introduced species, *Leptopsylla segnis*, now cosmopolitan

on house mice *Mus musculus*. It is also recorded from native hosts including marsupials.

**9. Ceratophyllidae.** A large family with a holarctic distribution on birds and mammals. The genus *Ceratophyllus* is mainly holarctic with 63 species and subspecies, mostly bird fleas. Only *C. gallinae* occurs in Australia, and it is thought to have been introduced with domestic poultry. *Nosopsyllus* has 61 species and subspecies in the Palaearctic, Ethiopian and Oriental regions; 2 species, now cosmopolitan on commensal rats and mice, occur in Australia.

ACKNOWLEDGMENTS. We are greatly indebted to Mr R. M. Warneke, Fisheries and Wildlife, Conservation, Forest and Lands Department, Heidelberg, for permission to quote from his unpublished studies of *Uropsylla tasmanica*. Valuable comments on drafts of this chapter were provided by Dr R. E. Lewis, Department of Entomology, Iowa State University, Ames, U.S.A. and Prof. R. L. C. Pilgrim, Department of Zoology, University of Canterbury, Christchurch, New Zealand.



# Diptera

(Flies)

D. H. COLLESS and D. K. McALPINE

Endopterygote Neoptera, with a pair of membranous wings on mesothorax only, the metathoracic pair represented by club-like halteres; prothorax and metathorax greatly reduced; mouth-parts of adults suctorial, often adapted for piercing. Larvae without true legs. Pupae adecticous and obtect or exarate, the latter in a puparium.

The Diptera form one of the larger insect orders, the world total of species, described and undescribed, probably being at least 150 000. Despite a considerable diversity of structure, almost all adults are immediately recognisable by the presence of only one pair of functional wings. The exceptions are the relatively few apterous species, which have other attributes, of mouth-parts, thorax, etc., that indicate their proper relationships. Such characters also distinguish the Diptera from the few other insects (some Ephemeroptera, some Derbidae, male Coccoidea) that have only two wings.

The order includes many common and familiar insects: mosquitoes, midges, sand flies, house flies, blowflies, etc. Some are important pests or vectors of disease, but others are beneficial, and, by virtue of their parasitic or predatory habits, play an important role in regulating the populations of many plants and animals that adversely affect human welfare. We may also note our special debt to the inconspicuous *Drosophila*, to which we owe so much of our basic knowledge of cytogenetics and genetic mechanisms.

Important general works include those on anatomy by Séguy (1951), on the immature stages by Hennig (1948–52), Brauns (1954) and Ferrar (1988); on cytology by M. J. D. White (1949) and Boyes (1958); and on biology by Séguy (1950, 1951) and Oldroyd (1964). Important regional monographs include those by Lindner (1924– ), for the Palaearctic; Griffiths (1980– ) and J. F.

McAlpine *et al.* (1981–89), for the Nearctic; Hardy (1960–81) for Hawaii, Harrison (1959) for New Zealand, and Bezzi (1928) for Fiji; also, the series *Fauna of (British) India, Diptera of Patagonia and South Chile*, and *Insects of Micronesia*. Much of the world fauna has been catalogued: in Soós and Papp (1984– ) (Palaearctic); Stone *et al.* (1965) (Nearctic); Departamento de Zoologia, São Paulo (1966– ) (Neotropical); Crosskey *et al.* (1980) (Afrotropical); Delfinado and Hardy (1973–77) (Oriental); and Evenhuis (1989) (Australasian and Oceanic).

## Anatomy of Adult

For reasons that are largely historical, we lack a completely uniform, standard terminology for the external anatomy of the Diptera. Various special terminologies apply within limited groups of families, or in different parts of the world. However, there is little confusion in practice. The terminology recommended below is based largely in the classical treatise by Crampton (1942) and is practically identical with that used in the 1st edition of this work. Recent, much more detailed treatments are available in Hennig (1973) and J. F. McAlpine *et al.* (1981); but despite the excellence of those works, we have not always followed them. We prefer sometimes to adhere to long established usage, in the belief that some terms are destined to remain conventional or topographical, rather than based strictly in morphological theory.

**Head** (Fig. 39.1). A highly mobile, relatively large

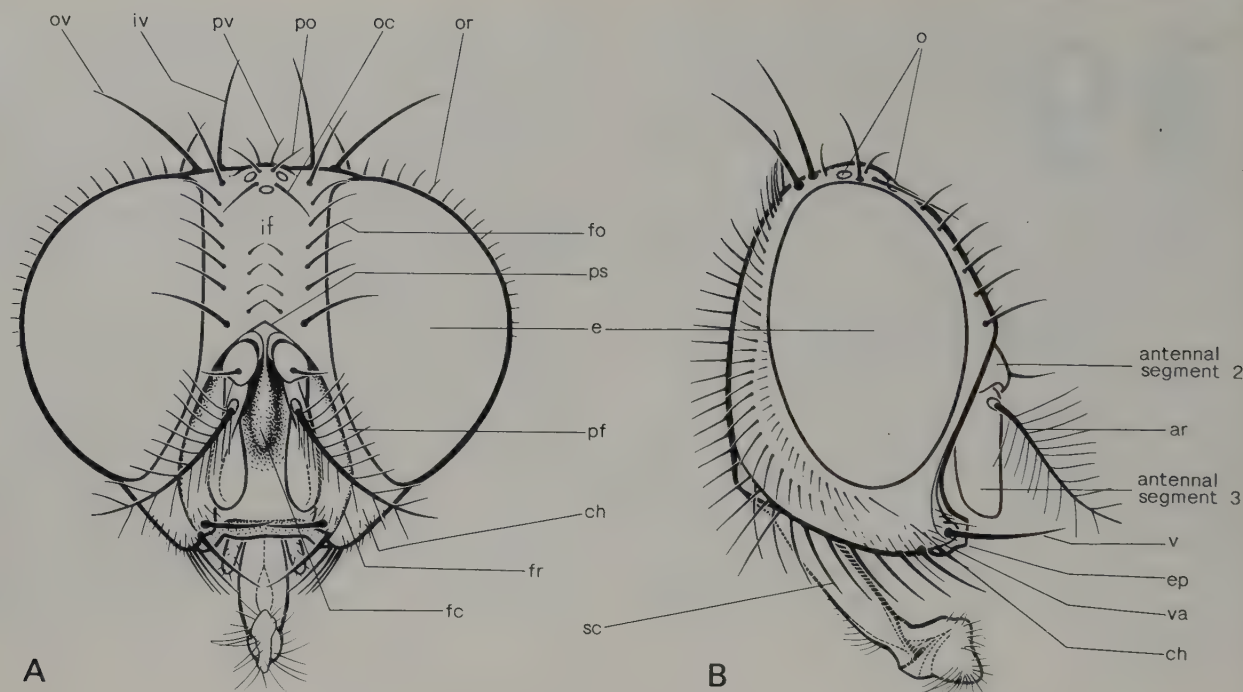


Fig. 39.1 Head of muscoid fly: A, anterior; B, lateral.

[T. Binder]

ar, arista; ch, cheek; e, eye; ep, epistoma; fc, facial carina; fr, facial ridge; o, ocellus; pf, parafrontal; ps, ptilinal suture; va, vibrissal angle. Bristles: fo, fronto-orbital; if, interfrontal; iv, inner vertical; oc, ocellar; or, orbital; ov, outer vertical; po, postocellar; pv, postvertical; sc, subcranial; v, vibrissa.

capsule, its parts defined principally by reference to the occipital foramen, median ocellus, insertions of antennae, margins of eyes and oral region, and the anterior tentorial pits. The tentorial pits may be poorly, or not at all, developed, particularly in the Cyclorrhapha. They are best seen in the Orthorrhapha, and completely penetrate the head in some Stratiomyidae (e.g. *Boreoides*), the arms of the tentorium forming a pair of hollow tubes.

The *occiput* may be flattened or concave in higher Diptera, with a distinct *median sclerite* (epicephalon, cerebrale). The *vertex* is of rather indefinite extent, but the ocelli may be borne on a distinct *vertical* or *ocellar triangle*, often raised and defined by grooves, then better termed *ocellar tubercle*. The median ocellus, when present, marks the dorsal limit of the true frons, which, strictly, includes all the anterior surface down to the clypeus. However, students of the higher Diptera traditionally restrict the term to include only the area dorsal to the antennae (strictly, the postfrons). The *frons*, in this restricted sense, may be differentiated into a median *interfrons* (frontal stripe or vitta) and *orbital plates* (parafrontals, fronto-orbitals) adjacent to the eyes. In the Schizophora, a transverse *ptilinal fissure* crosses just above the antennae and extends down laterally, in the form of an inverted U, towards the clypeus.\* It represents the closed lips of the *ptilinum*, an eversible sac used in eclosion, and often cuts off a small oval or crescentic *frontal lunule* above the bases of the antennae.

The area below the antennae is the *face*, a general term

for the anterior frons, which is bounded ventrally by the fronto-clypeal or epistomal suture; or, if this is absent, by the level of the tentorial pits. Running dorsally from the pits, a pair of *frontogenal sutures* mark off a median *facial plate*, while in Schizophora the ventral arms of the ptilinal fissure continue down to divide the lateral strips into the *parafrontals*, adjacent to the eyes, and the more medial *facialia*. The latter term is also applied to the similar, but not homologous, strips between the eyes and the enlarged clypeus in, e.g., Tabanidae. These would be better termed *genae*, but that term is generally restricted to the more ventral areas (cheeks, jowls, buccae) below the level of the eyes. In Schizophora the antennae may lie on the face in longitudinal grooves, the *antennal fossae* (or foveae), separated by a median ridge, the *facial carina*; or the whole face may be sunken. In such cases the raised facialia form the *facial ridges*, which usually terminate ventrally in prominences, the *vibrissal angles*, each bearing one or more stout bristles or *vibrissae*. Between the vibrissal angles, there may be differentiated a projecting *epistoma*, which is probably the postclypeus and, strictly, not part of the face. Below the face, the clypeus or anteclypeus ('prelabrum') is usually distinct, sometimes borne on the proboscis. The cavity into which the proboscis is retracted, often miscalled the 'oral cavity', is the *subcranial cavity*, and its margin the *subcranial margin*. The posteroventral region of the head-capsule is formed by the postgenae, often joined by a sclerotised region, the *pseudogula*.

The compound eyes may be dichoptic (separated) or holoptic (contiguous). The holoptic condition is typically seen in males; or in both sexes in families such as the

\* A transverse groove may occur in other Diptera, but it rarely continues below the antennae.



Acroceridae and Pipunculidae, in which the eyes may occupy most of the surface of the head. In some Nematocera (Sciaridae, Cecidomyiidae) the eyes are connected above the antennae by a narrow line of facets, or *eye-bridge* (Fig. 39.20C). Sometimes each eye is differentiated into dorsal and ventral components by a difference in facet size or by a transverse groove. In the cecidomyiid *Trisopsis*, the components are completely separated, and the dorsal parts contiguous, giving a three-eyed appearance, while in *Perissomma* (Fig. 39.18D) all four parts are completely separated. Many Diptera have small hairs between the facets, for which we propose the term *ommatrichia*; these sometimes produce a marked pilosity over the whole eye. There are typically 3 ocelli, but the median one, or all 3, may be absent.

The antennae (Fig. 39.2) vary considerably in structure, and may exhibit strong sexual dimorphism. The simplest type is filiform, with 16 segments, but the number can be greater or, particularly in the Brachycera, much less. The scape may be rudimentary (e.g. in the Culicidae), while in many Nematocera the pedicel is distinctly enlarged and

the remaining, flagellar segments more or less uniform in size and shape. In most higher Diptera, the 3rd segment is enlarged to some degree and the more distal segments reduced and appearing as a mere appendage. When fine and bristle-like, the appendage is termed an *arista*; when stouter and more rigid, a *style*; its segmentation may or may not be apparent. In many Diptera, the pedicel (torus) encloses Johnston's organ, a group of receptors which serve to detect air vibrations.

The mouth-parts (Fig. 39.3) are adapted for sucking, and form a more or less elongate *proboscis* or *rostrum*, which usually incorporates the labrum, and sometimes elements of clypeus and even of frons, as in *Elephantomyia* (Tipulidae) and *Neoantlemon* (Mycetophilidae). The labrum (labrum-epipharynx) may be small and flap-like, but it is normally more or less elongated to form the roof of the food canal. The floor of the canal is formed either by the overlapping mandibles or by the elongate, deeply grooved hypopharynx into which the salivary duct opens basally. The mandibles, usually absent in males and often so in females, are found mainly in predatory species

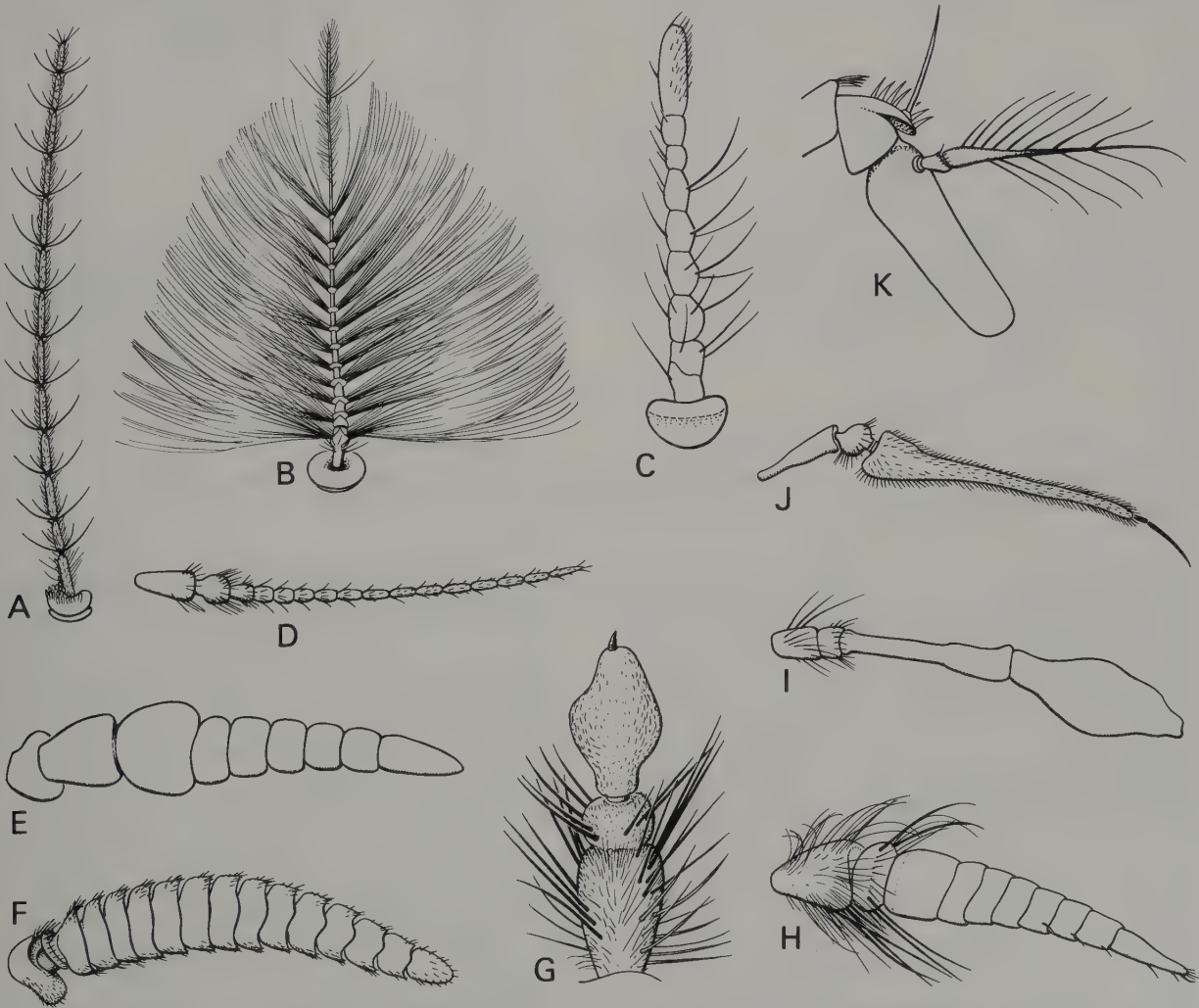


Fig. 39.2 Antennae of various Diptera: A, *Aedes alternans*, Culicidae, ♀; B, *A. alternans*, ♂; C, *Heptagyia tasmaniae*, Chironomidae, ♀; D, *Sylvicola dubius*, Anisopodidae, ♀; E, *Austrosimulium bancrofti*, Simuliidae, ♀; F, *Keroplatus mastersi*, Mycetophilidae, ♂; G, *Apiocera asilica*, Apioceridae, ♀; H, *Scaptia maculiventris*, Tabanidae, ♀; I, *Miltinus viduatus*, Mydidae, ♂; J, *Rhabdium pudicum*, Dolichopodidae, ♂; K, *Musca vetustissima*, Muscidae, ♂.

[T. Binder]

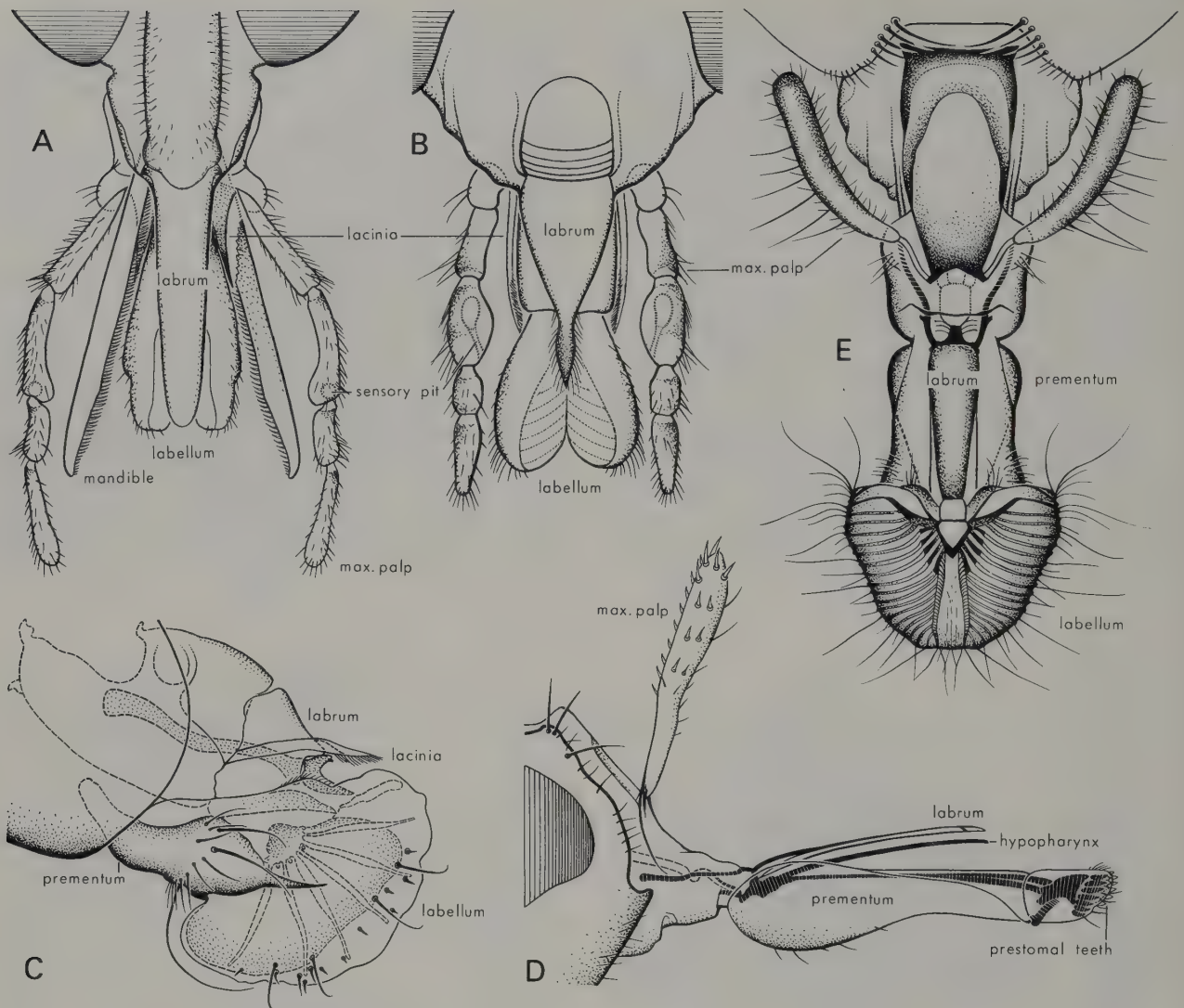


Fig. 39.3 Mouth-parts of various Diptera (all ♀♀): A, *Edwardsina* sp., Blephariceridae, dorsal; B, *Sylvicola dubius*, Anisopodidae, dorsal; C, *Heteropsilopus cingulipes*, Dolichopodidae, lateral, palp not shown; D, *Haematobia exigua*, Muscidae, lateral; E, *Calliphora stygia*, Calliphoridae, dorsal. [T. Binder]

as long, piercing stylets. The maxillae have their basal sclerites reduced and fused into the structure of the proboscis. The free portions comprise the slender, elongate lacinia, which is toothed or pointed in most predators, or, in many Nematocera, brush-like at its apex; and the 1–5-segmented palp, which may bear *sensory pits* or *plaques*. The labium is the largest of the mouth-parts, and both mentum and prementum may be distinct; in the proboscis of many Cyclorrhapha, the prementum forms a conspicuous ventral sclerite, sometimes called the *theca*. The labial palps are represented by the *labella*, a pair of apical lobes on the prementum. In some lower or predatory forms, they are slender and 2-segmented; but in higher forms, they become a pair of inflated membranous lobes (sometimes fused), with their surfaces traversed by a series of sclerotised canals, the *pseudotracheae*, which may bear *pseudotracheal teeth*, or be replaced by *prestomal teeth* (Elzinga and Broce 1986). The piercing type of proboscis found in predators and blood-suckers is

functionally the primitive one, having been independently lost, and perhaps redeveloped, on a number of occasions (Downes 1958; Downes and Colless 1967). Usually the labrum and hypopharynx, and, variably, the laciniae and mandibles form a set of elongate *stylets*, wrapped within a groove in the labium; the latter is usually fleshy (e.g. Culicidae, Fig. 39.4), but may itself also be sclerotised to form a piercing organ (e.g. *Haematobia*, Fig. 39.3D).

Chaetotaxy of the head is shown in Figure 39.1.

**Thorax** (Fig. 39.5). Both pro- and metathorax are greatly reduced, and the mesothorax correspondingly enlarged to accommodate the muscles of the single pair of wings. The principal thoracic landmarks are the meso- and metathoracic spiracles, and the attachments of wings, halteres and legs.

The cervix (neck) is a largely membranous area of modified prothorax, and bears at least one lateral pair of *cervical sclerites*. The pronotum is usually clearly divided into anterior and posterior parts; the *anterior pronotum*



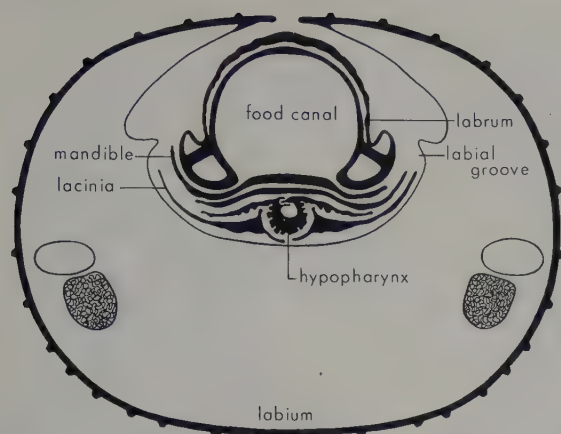


Fig. 39.4 Transverse section towards apex of proboscis of *Aedes aegypti*, Culicidae (from electron micrograph prepared by B. K. Filshie).

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is best developed in lower Diptera (e.g. Tipulidae, Bibionidae) and may consist of a narrow collar and/or a pair of prominent *pronotal lobes*, whereas the *posterior pronotum*, better developed in higher forms, is usually intimately associated with the mesonotum to form the *humeri* (postpronotum, humeral calli). Laterally, the episternum (*propleuron*) is normally distinct, but the epimeron may merge completely with the mesopleuron. The principal sternal sclerite is the basisternum (*proster-num*), lying a little anterior to the bases of the coxae. It may connect with the episternum via a narrow *precoxal bridge* (e.g. Culicidae, Bibionidae), or the two sclerites may be broadly fused (e.g. certain Empididae and Therevidae).

Enlargement of the mesothorax has resulted in distortion, and the homologies of its sclerites are not readily apparent. The mesonotum is, strictly, its entire dorsal surface, but the term has been traditionally restricted to the larger, anterior, wing-bearing plate (*scutum*, alinotum) only. The scutum is frequently divided by a transverse sulcus or 'suture' (V-shaped in Tipulidae) into 'prescutum' and 'scutum' (again not strictly correct morphologically), between the lateral parts of which there may be a triangular, sunken *notopleural area*. The *humeral pits* lie anteriorly on each side. In Nematocera and many Orthorrhapha, a narrow lateral sclerite, the *paratergite* (a vestige of the true prescutum), is differentiated in front of the wings, while, in Brachycera, the posterolateral angles of the scutum form the *postalar calli*. The *scutellum*, a clearly defined, rounded or triangular lobe, bounds the scutum posteriorly, and is sometimes preceded by a small ridge, originally termed *proscutellum*, but for obvious reasons better termed *prescutellum*.

Even more confusing terminologies have been applied to the parts below and behind the scutellum. They probably represent the intersegmental acrotergite, and should preferably be termed the *postnotum*; 'postscutellum' (see below) has also been used, and even (quite incorrectly) 'metanotum'. The postnotum is divided longitudinally into a median *mediotergite* and lateral *pleurotergites* or laterotergites; the latter (sometimes mis-called 'meta-

pleura') extend down to the metathoracic spiracle and may be divided into a dorsal *anatergite* and ventral *katatergite*. The anterior region of the mediotergite is usually concave but, particularly in Tachinidae, may be differentiated as a convex transverse ridge or lobe, the *subscutellum* (post-scutellum); its anterior portion may be membranous.

The mesothoracic spiracle lies towards the dorsal margin of the pleuron, near the junction of pronotum and mesonotum. The mesopleuron is divided by the vertical *pleural suture*, which runs more or less directly from wing base to coxa in most Nematocera, but becomes markedly zigzag in higher forms. It may include a distinct *midpleural pit*. The episternum comprises a dorsal *anepisternum* (*mesopleuron*) and ventral *katepisternum* or *sternopleuron*, the former often divided by a vertical *anepisternal cleft*, which may lie posteriorly, very close to the true pleural suture. The two sternopleura are often contiguous ventrally, fusing with or displacing much of the small sternum. The epimeron commonly has its dorsal *anepimeron* or *pteropleuron* clearly demarcated; the *katepimeron* (barette) is usually small, or fused with the detached meron of the coxa to form a composite *meropleuron* (*hypopleuron*); but the meron is distinct in some Nematocera.

The metathorax may be so reduced as to be almost vestigial. The metanotum forms a narrow, transverse strip (best developed in some Psychodidae and apterous Micropezidae), with the halteres arising from its lateral margins. The true metapleuron, lying below and behind the metathoracic spiracle, is not always clearly separated from the mesopleural sclerites, but when moderately developed, as in some Nematocera, it may be divided into *anepisternum*, etc. It, or its *katepisternum*, has also been included under the label of 'hypopleuron'. The true metasternum is usually greatly reduced, but may be distinct.

The thoracic endoskeleton is well developed to support the powerful flight muscles. Although largely ignored by taxonomists, it offers some useful characters. Its principal structures are: the paired sternal apophyses, arising from the sternal plates and, in the meso- and metathorax, fused basally to form complex *furcae*; the *pleural arms*, arising from the mesopleural suture; and the mesothoracic *prephragma* and *postphragma*. The prephragma, at the anterior margin of the mesonotum, is often small or vestigial, but the postphragma is well developed as an internal, posterior extension of the postnotum. Its primitive bilobed condition is preserved in most Tipulomorpha and Culicomorpha, but in most other families it forms a convex plate, almost completely closing the thoracic cavity; in some, e.g. Scatopsidae, it projects deeply into the abdomen.

The chaetotaxy of the thorax is shown in Figure 39.5.

**Legs** (Fig. 39.6). There is great diversity of leg structure in the Diptera, and there are examples of striking modifications on all segments. The adaptive significance, if any, is often obscure (e.g. the male coxal processes in some *Mycomya* spp., Mycetophilidae), but some serve a sexual function (D. K. McAlpine 1973b).

The coxae are usually rather small, though the fore

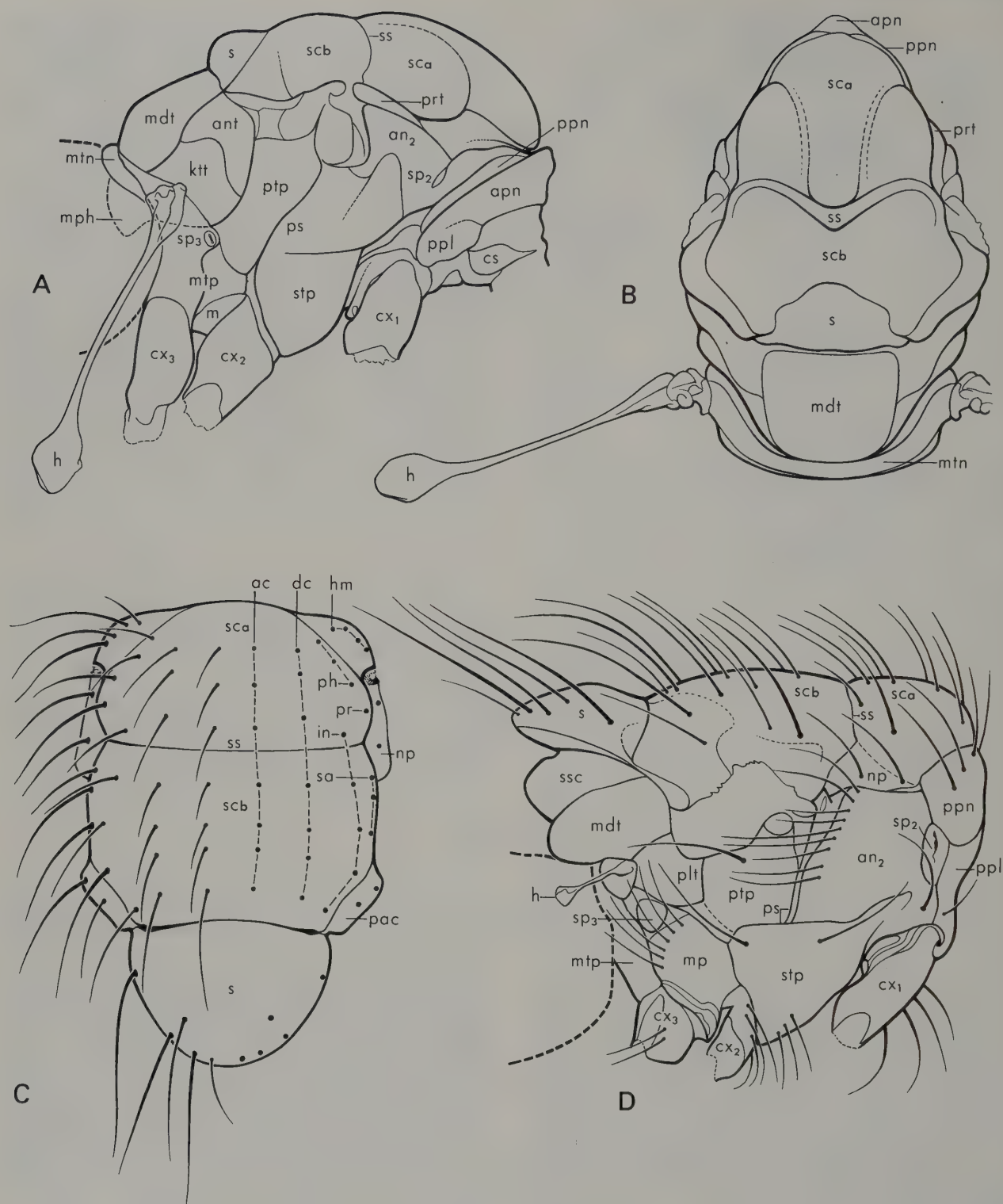


Fig. 39.5 Thoracic structure and chaetotaxy: A, B, Tipulidae, lateral and dorsal; C, D, Tachinidae, dorsal and lateral.

[T. Binder]

an, anepisternite (mesopleuron); ant, anatergite; apn, anterior pronotum; cs, cervical sclerite; cx, coxa; h, haltere; ktt, katatergite; m, meron; mdt, mediotergite; mp, meropleuron; mph, mesopostphragma; mtp, metapleuron; mtn, metanotum; np, notopleuron; pac, postalar callus; plt, pleurotergite; ppl, propleuron; ppn, posterior pronotum; prt, paratergite; ps, pleural suture; ptp, pteropleuron; s, scutellum; ssa, ssa, presutural and postsutural parts of scutum or mesonotum; sp, spiracle; ss, scutal or mesonotal suture; ssc, subscutellum; stp, sternopleuron. Subscript numbers 1–3 indicate pro-, meso- and metathorax, respectively. Bristles (in C): ac, acrostichal; dc, dorsocentral; hm, humeral; in, intraalar; ph, posthumeral; pr, presutural; sa, supraalar.



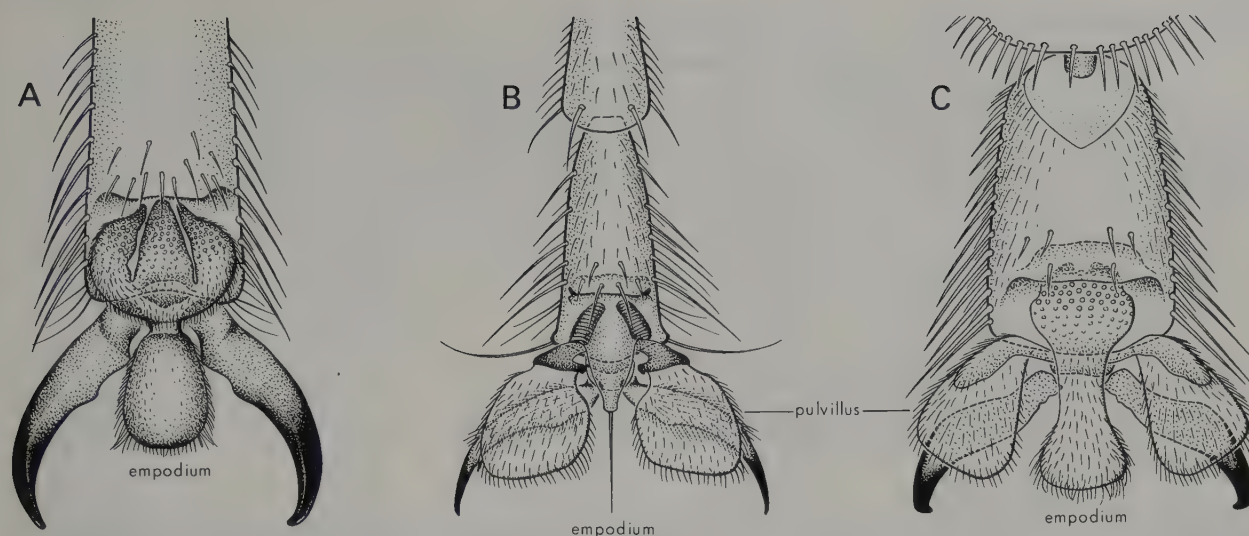


Fig. 39.6 Tarsal and associated structures: A, *Clytocosmus helmsi*, Tipulidae; B, *Musca domestica*, Muscidae; C, *Inopus rubriceps*, Stratiomyidae.

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coxae are often lengthened and sometimes swollen, while all three are characteristically elongate in the Mycetophilidae. In almost all Diptera, the articulation of the fore legs is quite different from that of the mid and hind legs, because of the greater mobility of the fore coxae. The mid coxa may possess a distinct meron, but it is normally fused into the pleuron, particularly in higher Diptera. The trochanter is usually small.

The femur and tibia are the longest segments of the leg, and normally subequal, with the femur rather stout and flattened and the tibia more slim and cylindrical. In some Empididae and Ephydriidae the fore femur and tibia are modified in an apparently raptorial, mantid-like fashion, while a few species in various families have the mid or hind legs thus modified. In many families, particularly of Nematocera, the tibiae may bear *apical combs* of close-set setulae and/or one or two articulated *spurs*.

The tarsi typically consist of 5 segments, which may be variously modified, principally by thickening or flattening; the basal segment (*basitarsus* or *metatarsus*) and sometimes other segments may also bear apical combs. The distal segment bears a pair of *claws* (ungues), usually simple but sometimes toothed. Beneath the claws there may be a pair of pad-like *pulvilli* and/or a median *empodium* (Fig. 39.6), the latter often bristle-like but sometimes, e.g. in Bibionidae and Tabanoidea, pulvilliform. Many flies secrete on the pulvilli and pulvilliform empodium an adhesive substance that enables them to cling to smooth surfaces.

**Wings** (Fig. 39.7). The functional wings are borne on the mesothorax, the metathoracic pair having become reduced to small, club-like structures, the *halteres* (Fig. 39.5). Both wings and halteres may be lost. The original four-winged condition is partially restored in certain *Drosophila* mutants, and is still recognisable in some pupae and primitive Nematocera. The halteres vibrate rapidly during flight, and are believed to act as gyroscopic sense organs of balance, precessional forces being detected by arrays of sensilla near their bases.

The base of the wing includes a series of axillary sclerites, of which the most conspicuous are the tegula (*epaulet*) at the extreme base of the anterior margin, and the adjacent, more distal humeral plate (*basicosta*, *subepaulet*). Posteriorly, the membrane may have up to three basal lobes; the *upper* and *lower calypters* or *squamae*, which are folded one above the other; and the more distal *alula* or axillary lobe which, when differentiated, is marked off by a deep *axillary incision*. The lower calypter is immobile, with its margin continuing on to the notum; it may be vestigial, particularly in Nematocera, but in many Tabanoidea and Cyclorrhapha it is greatly enlarged, roofing over the hollow in which the halteres lie. Distal to the axillary incision there may be a distinct anal lobe. The membrane of the wing may be hyaline or may bear distinctive colour patterns. The disposition of micro- and macrotrichia on the membrane, and of the latter on the wing veins, are important taxonomic characters.

The hypothetical venation of the primitive dipteran is shown in Fig. 39.7A, and its modifications in subsequent figures. As the older Loew-Williston and Schiner notations have been extensively used by dipterists, their equivalents in the modified Comstock-Needham system are shown in Table 39.1. Several interpretations have been proposed for the radial and cubital fields (C. P. Alexander 1929; Hennig 1954; J. F. McAlpine *et al.* 1981), but we prefer here to follow the more conservative interpretations shown. The anomalous convexity of the posterior branches of Rs and M possibly arose through incorporation in them of MA and a primitive anterior branch of CuA respectively, while M, as used here is strictly MP. This being so, it would seem inconsistent to follow J. F. McAlpine *et al.* (1981), who retain our R<sub>5</sub> but interpret our M<sub>4</sub> as CuA<sub>1</sub>.

Amongst the more characteristic features of the primitive venation are: (a) the 'kink', constriction, or sulcus in R close to the level of the humeral vein, marking off a basal section, the *stem-vein*; (b) the transverse fold, often vein-like, forming a *brace* ('arculus') between M or Cu

Table 39.1 Comparison of systems of wing venation applied to the Diptera

Veins			Cells		
Modified Comstock-Needham (Fig. 39.7)	Loew-Williston	Schiner	Modified Comstock-Needham (Fig. 39.7)	Loew-Williston	Schiner
C	Costa	Costa	C	Costal	Costal
Sc	Auxiliary	Mediastinal	Sc	Subcostal	Mediastinal
R <sub>1</sub>	1st longitudinal	Subcostal	R	1st basal	1st basal
R <sub>2</sub>	} 2nd longitudinal	} Radial	R <sub>1</sub>	Marginal	Subcostal
R <sub>3</sub>			R <sub>3</sub>	1st submarginal	1st cubital
R <sub>4</sub>	} 3rd longitudinal	} Cubital	R <sub>4</sub>	2nd submarginal	2nd cubital
R <sub>5</sub>			R <sub>5</sub>	1st posterior	1st posterior
M <sub>1</sub>	} 4th longitudinal	} Discal	M	2nd basal	2nd basal
M <sub>2</sub>			Discal (median, 1st M <sub>2</sub> )	Discal	Discoidal
M <sub>3</sub>	} 5th longitudinal (branches)	} Postical (incl. <i>m-cu</i> )	M <sub>1</sub>	2nd posterior	2nd posterior
M <sub>4</sub> (Cu <sub>1</sub> , Cu <sub>1a</sub> )			M <sub>2</sub>	3rd posterior	3rd posterior
CuA (Cu <sub>1</sub> )	5th longitudinal (base)		M <sub>3</sub>	4th posterior	4th posterior
CuP (Cu <sub>2</sub> )	—	—	M <sub>4</sub>	5th posterior	5th posterior or postical
1A	6th longitudinal	Anal	CuP (CuA+CuP)	Anal	3rd basal or anal
2A	Axillary	Axillary	1A	Axillary	Axillary

and the apex of the stem-vein (we regard this as a strut, formed along a bending-line, as sometimes seen elsewhere in the wing; J. F. McAlpine *et al.* 1981, interpret it as the trace of vein MA); (c) the well defined 'discal' ('median') cell; (d) the reduction of CuP to little more than a concave fold; (e) the presence of only two anal veins. The primitive pattern is most closely approached by the Tanyderidae, and the most characteristic lines of specialisation are: (a) shortening of the costa to end near or proximal to the wing apex; also, development of constrictions or breaks towards its base; (b) loss of branching and the apical portion of Sc; (c) reduction in branching of Rs and/or a basal shift of its origin; R<sub>2+3</sub> is normally branched only in the more primitive Nematocera; (d) loss of *i-m* and hence of the discal cell; (e) reduction of branching of M, or loss of its basal portion, or detachment of M<sub>3+4</sub> which may appear to fork from CuA; (f) shortening of CuA, and flexion of its apex to end in 1A; (g) shortening or loss of 2A, and sometimes 1A also—2A is very short, rudimentary, or absent in all but Tipulidae. Almost all these trends are towards reduction of the venation, particularly in the posterior field, and are presumably correlated with improvements in the dynamics of two-winged flight.

**Abdomen.** The principal landmarks are: the spiracles, borne within, or just below, the lateral margins of the tergites; the male and female genital orifices; the cerci; and the anus. Primitively, there are 11 segments, but 10 and 11 are generally fused to form a composite *proctiger* (or, simply, segment 10) which bears cerci and anus. In higher Diptera, there is also a progressive tendency towards reduction of segment 1 and fusion of tergites 1 and 2. Most Diptera show some degree of telescoping of the terminal segments, but in higher forms, particularly

Cyclorrhapha, the more posterior segments are clearly differentiated as a slender *postabdomen*, retracted within, or curved beneath, the broader *preabdomen*. The postabdomen may be strongly modified, particularly in males. The convenient, general designation *terminalia* is applied to the terminal complex of modified genital and anal segments *plus* any adjacent segments that show modifications for copulation or oviposition; it may include the entire postabdomen. 'Hypopygium' and 'genitalia' should not be used as synonyms of 'terminalia'; their meanings are much more restricted.

**FEMALE TERMINALIA** (Fig. 39.8). These structures are usually relatively simple. In many families, segments 6 and 7 are reduced and, together with the more posterior segments, form a telescopic, eversible, tubular ovipositor (Fig. 39.8B). However, in a few (e.g. Agromyzidae, Tephritidae), the fused sclerites of segment 7 form an ovipositor sheath, which is stout, rigid and permanently exerted, while the terminal segments are adapted for piercing (Fig. 39.8C). In many Nematocera and Orthorrhapha, S8 is produced posteriorly and may be bilobed; in the complex ovipositor of many Tipulidae, those lobes are produced to form the *sternal* (hypogynial) *valves* ('gonapophyses'), the *tergal valves* being formed by the cerci (Fig. 39.8A). The oviduct opens behind S8, and its distal portion may bear a rod-like or more complex sclerotisation, the *vaginal apodeme* or *furca*. Behind the genital orifice, there may be a series of small sclerites, derived mainly from S9, which are of taxonomic importance in some families. In many Orthorrhapha, T9 is longitudinally divided into a pair of hemitergites, the *acanthophorites*, which bear strong spines (Fig. 39.8D); in Cyclorrhapha, it tends to unite with the proctiger. The latter structure shows signs of segmental differentiation in



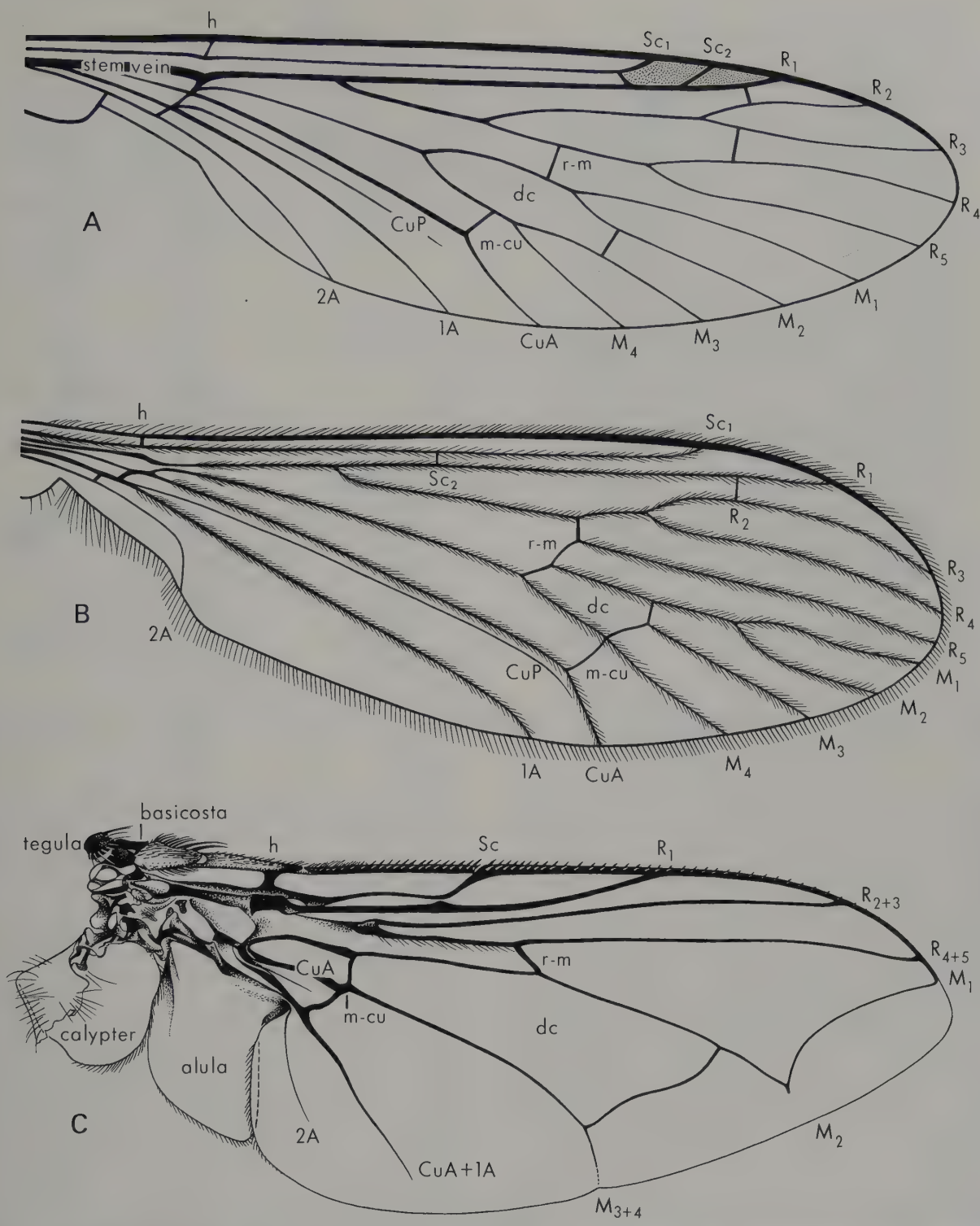


Fig. 39.7 Wing venation: A, reconstruction of hypothetical ancestor of Diptera (cf. Fig. 1.18A); B, tipuloid pattern, *Nothotrichocera cingulata*, Trichoceridae; C, muscoid pattern, *Chrysomya saffranae*, Calliphoridae. Standard notation for veins; dc, discal cell. [T. Binder]

some primitive forms, but normally appears as a single unit, composed of a dorsal *supra-anal plate* (epiproct) and a ventral *subanal plate* (hypoproct, postgenital plate); it bears the paired cerci, primitively 2-segmented, but sometimes reduced to tiny lobes or fused.

**MALE TERMINALIA** (Fig. 39.9). These structures are

often complicated, and the terminology of the parts has become exceedingly confused (see Crampton 1942; Zumpt and Heinz 1950; van Emden and Hennig, in Tuxen 1970b; Griffiths 1972; J. F. McAlpine *et al.* 1981). The basic pattern is best seen in the more primitive Nematocera (Fig. 39.9A), in which homologies are fairly

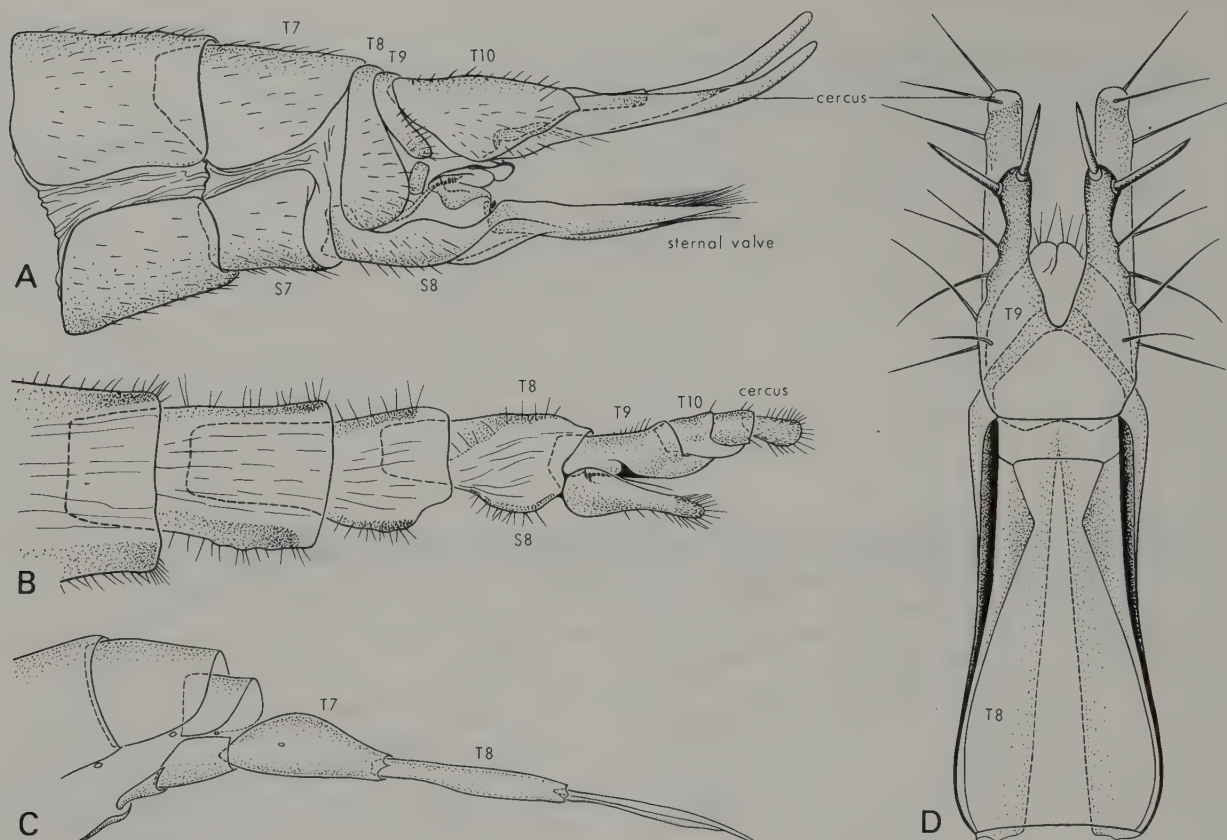


Fig. 39.8 Female terminalia: A, *Gynoplistia* sp., Tipulidae, lateral; B, *Sciara* sp., Sciaridae, lateral; C, *Dacus tryoni*, Tephritidae, lateral; D, *Heteropsilopus cingulipes*, Dolichopodidae, dorsal. [T. Binder]

clear; but, ascending through the Orthorrhapha (Fig. 39.9C) considerable modifications occur until, in the Cyclorrhapha (Fig. 39.9B), homologies become obscure and are still disputed. In the simplest types, modifications are largely restricted to segment 9 and the proctiger, apart from reductions associated with telescoping of segments 7 and 8, and occasional development of lobes, spines, etc. ventrally on segment 8 (pregenital segment, *protandrium*). Segment 9 (genital segment, *andrium*) is considerably modified; its tergite (*epandrium*) may be reduced or enlarged, sometimes bearing articulated processes, the *surstyles*, while the sternite (*hypandrium*) bears the usually forcipate *coxites* (gonocoxites, basistyles, side-pieces), each with an apical *style* (gonostylus, dististyle, clasper), and the median copulatory organ, the *aedeagus*. The coxites may bear various accessory lobes or appendages (e.g. the *claspettes* of Culicidae) while the style may be double (as in, e.g., Tipulidae) or branched. S9 is often greatly reduced, and may be fused with the coxites.

The name 'aedeagus' seems the best available general term for the copulatory organ (also called phallosome, mesosome, penis). This structure exhibits an enormous variety of forms, from a membranous or sclerotised lobe or tube, up to the complex 'phallosome' of some Culicidae. This is due, in part, to incorporation of a variety of elements, including intersegmental sclerotisations and internal lobes of the 'parameres' (Abul-Nasr 1950).

The latter may not be the structures so designated in Coleoptera and accepted by Snodgrass (1957), and are best referred to as *parandrites*; they may remain distinct (e.g. in *Chironomus* and *Trichocera*) as appendages flanking the aedeagus. The proctiger usually forms a distinct unit bearing a pair of 1-segmented cerci.

In some Nematocera and Orthorrhapha, segment 9 and the proctiger are temporarily or permanently rotated through 180°, so that true ventral structures lie in a dorsal position. Such a condition is readily recognised by reference to the proctiger and aedeagus. A somewhat similar rotation occurs in certain Empididae, but only through about 90°, and associated with considerable asymmetry of the parts. In Dolichopodidae and Cyclorrhapha, the rotation has proceeded through 360°, restoring the original relations of anus and genital structures, a process called *circumversion*. The 'torsion', which takes place in the pupa, may affect the entire postabdomen, causing a sinistral displacement of the sternites, with S8 usually adopting a dorsal position (laterally, to the left of segment 9, in Dolichopodidae). In some forms, however, external symmetry is restored (e.g. Ephydroidea). The circumverted terminalia are nearly always folded forward ventrally against the preceding sternites.

In these higher Diptera (Fig. 39.9B), S5 often bears a prominent pair of *pregenital* ('copulatory') lobes, while the coxites are greatly reduced or absent. Dorsally, the displaced sternites of segments 7 and 8 may fuse to form



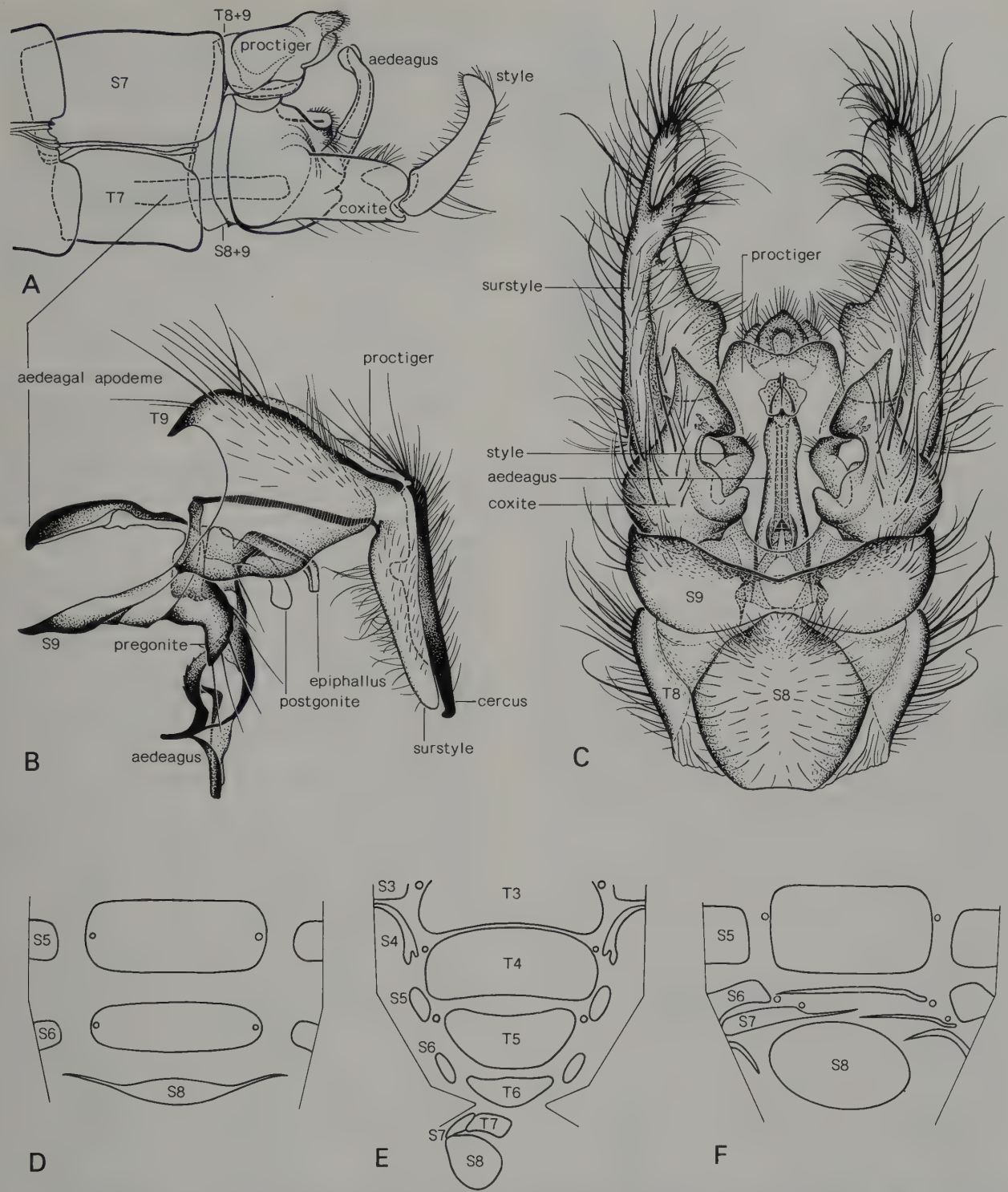


Fig. 39.9 Male terminalia: A, *Eutanyderus wilsoni*, Tanyderidae, lateral, ventral surface uppermost; B, *Calliphora stygia*, Calliphoridae, lateral; C, *Neoaratus hercules*, Asilidae, ventral. Protandrograms: D, Teratomyzidae, undescribed; E, *Paraclius* sp., Dolichopodidae; F, *Dasycoelopa australis*, Coelopidae. [A–C by T. Binder; D–F by A. Hastings]

a composite protandrium (a *protandrogram*, e.g. Fig. 39.9D–F, is a diagram showing the development and disposition of the postabdominal sclerites and their associated spiracles). The most prominent appendages are the *surstyles* (lateral valves) of T9 and the *cerci* (medial valves), the latter being sometimes partly fused. S9 is

sometimes reduced, but may be inflected to form a *hypandrial apodeme*. The aedeagus exhibits a variety of bizarre forms (e.g. the coiled, ribbon-like form in Tephritoidea), and is often differentiated into *basiphallus* (phallobase) and *distiphallus* (phallus, aedeagus), the former bearing a posterior, spine-like *epiphallus* (gonacan-

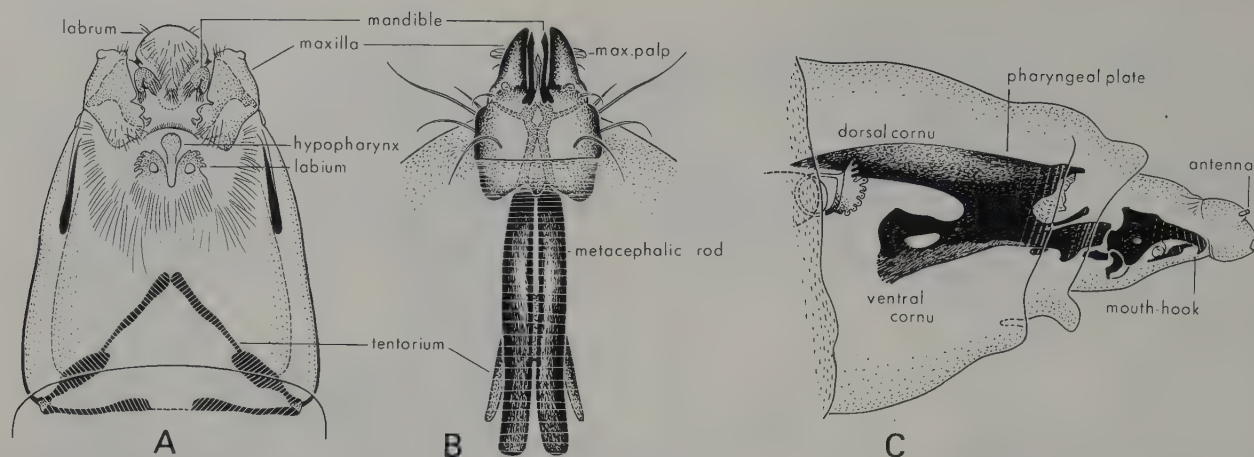


Fig. 39.10 Larval heads and mouth-parts: A, *Sylvicola dubius*, Anisopodidae, ventral; B, unidentified sp. of Asilidae, dorsal; C, *Calliphora vicina*, Calliphoridae, lateral.  
[T. Binder]

thus, spinus titillatorius). At the base of the aedeagus, there are often 2 pairs of small appendages, the *pregonites* and *postgonites* (anterior and posterior 'gonapophyses'), which are presumably derived from the coxites and parandrites; also, internally, there is usually a strong *aedeagal apodeme*.

**Internal Anatomy.** The alimentary canal has the buccal cavity dilated and lined with several small sclerites; attached dilator muscles operate the cavity as a pump to draw up fluid through the mouth-parts. In the blood-sucking Tabanidae, Culicidae and Psychodidae (*Phlebotomus*), a similar *pharyngeal pump* is also present, and the sclerites of the two chambers in Culicidae and *Phlebotomus* form a *bucco-pharyngeal armature* which is of taxonomic importance. The tubular oesophagus bears usually 1, but sometimes 3, characteristic diverticula, of which the ventral one ('crop') forms a large, distensible sac lying mainly in the abdomen. It functions as a primary or secondary food reservoir, its contents passing slowly back to the gut; in mosquitoes, it stores only liquids other than blood, which passes directly through the gut. The mid gut is a simple sac in the lower Diptera, but highly convoluted in Cyclorrhapha. The hind gut terminates in a dilated rectum bearing 2, 4 or 6 papillae. There are generally 4 Malpighian tubules (2 in *Culicoides*, 5 in *Psychoda* and Culicidae). The salivary glands usually lie in the thorax, but may extend into the abdomen (e.g. in *Musca*); they are normally elongate and tubular, and may be branched (e.g. the trilobed glands of the Culicidae).

The nervous system shows a broad evolutionary sequence, from the generalised Nematocera with 3 thoracic and 7 abdominal ganglia (8 in the exotic Nymphomyiidae) to the higher Cyclorrhapha with all ventral ganglia fused; other groups show a variety of intermediate conditions. The respiratory system is notable for the development of greatly dilated air-sacs, mainly in the abdomen and particularly prominent in the Cyclorrhapha.

In the female, the ovaries are paired, and each comprises from 1 up to more than 100 polytrophic ovarioles, while up to 4 spermathecae and a series of accessory

glands open into the oviduct. In ovoviviparous and viviparous groups, the number of ovarioles is small, and the oviduct is dilated to form a *uterus*; in viviparous groups, the accessory glands secrete a milky fluid that nourishes the larva *in utero*. In the male, the testes are normally small, compact, ovoid bodies, often deeply pigmented; in 'pupiparous' groups, they take the form of compactly coiled, thread-like tubules. Their vasa deferentia join to form the ejaculatory duct, with which is often associated a muscular ejaculatory sac; paired accessory glands may also be present. A conspicuous sclerite, the *ejaculatory apodeme*, is often attached to the ejaculatory duct.

**Cytogenetics.** Compared with other orders, the Diptera have, in general, very few chromosomes. Most have from 3 to 6 pairs (usually 6 in higher forms), and none is known with more than 10 pairs; the homologous chromosomes generally form pairs during mitosis ('somatic pairing'). The male sex is almost always heterogametic, and X and Y chromosomes are commonly distinct, but in at least three lineages (limoniine Tipulidae, Psychodidae and Culicidae) they are barely, or not at all, apparent, presumably through fusion with autosomes (e.g. Breland 1961). In Nematocera, the X and Y chromosomes do not form bivalents at meiosis ('distance-pairing'), this probably being the primitive condition, but the Brachycera mostly show normal pairing. Another very distinctive feature is found in Bibionomorpha and Brachycera, which form no chiasmata during meiosis in the male, while the Cecidomyiidae and Sciaridae exhibit several strikingly bizarre features. A remarkable type of sex determination in the Phoridae has been described by Mainx (1964).

A characteristic feature of dipterous larvae is the presence of giant polytene chromosomes (e.g. Porter and Martin 1977) in the cells of the salivary glands and, to a lesser extent, other tissues. They are less common in adults, but have been found in various tissues, such as developing pulvilli (Whitten 1964), Malpighian tubules, and trichogen cells (Bedo 1986). They seem to occur in most families, but useful preparations have so far been demonstrated in only a few, their development being



apparently affected by larval nutrition. Such chromosomes have provided a powerful tool for genetic and cytotaxonomic research in the Diptera (e.g. J. Martin 1963; Bedo 1977; Lentzios *et al.* 1980).

Immature Stages

**Egg.** Generally small and elongate-oval. Being usually deposited in moist situations, the outer wall is normally pale and relatively thin. However, some have a strongly sclerotised chorion, which may be sculptured or developed into a plastron. Eggs are usually deposited singly or in irregular masses, but may be laid in well-defined rafts or rosettes (e.g. some *Culicidae*); or in a gelatinous matrix (most *Chironomidae*).

**Larva** (Figs 39.10, 12, 13, 14). The usual number of instars is 4, though more are recorded in some groups, whereas *Cecidomyiidae* have 3 and *Cyclorhapha* have the 4th instar suppressed. The notes below refer mainly to the mature larva.

Body form is variable, but usually more or less elongate, and cylindrical or dorsoventrally flattened. Macroscopically, the integument may appear smooth, but it usually bears rows of microscopic spines; these and any setae that may be present provide important taxonomic characters. Segmentation is normally distinct, into head, 3 thoracic, and 8 or 9 abdominal segments, but the apparent number may be reduced by fusion (e.g. *Blephariceridae*, *Lonchopteridae*) or increased by secondary division (e.g. *Anisopodidae*, *Therevidae*). True segmented legs are never present, but prothoracic and/or abdominal prolegs occur in some families (Figs 39.13F–H). In certain parasitic species of *Nemestrinidae*, *Acroceridae*, *Bombyliidae*, *Sarcophagidae* and *Tachinidae*, the active 1st instar larva is a planidium.

The Nematocera are generally *eucephalic* (Fig. 39.10A),

with a distinct head capsule formed from a median dorsal plate, the *cephalic apotome* ('frontoclypeus' of authors), separated by the *epicranial* 'suture' from the *lateral*, or *epicranial plates* (or *genae*); the latter curve under to form the sclerotised ventral wall of the capsule, and may meet or even fuse along the mid-line. The capsule is small and very weak in *Cecidomyiidae*, while the *Tipulidae* (Fig. 39.12C) have the more posterior parts weakly sclerotised and the head partially, or even completely, retracted into the prothorax. A rather similar *hemicephalic* condition is typical of most *Orthorrhapha*, in which the posterior portion of the head is retracted within the thorax, and usually represented by a dorsal pair of *metacephalic rods* or *plates*, a pair of *tentorial rods*, and a *pharyngeal skeleton* (Fig. 39.10B). The *Cyclorhapha* are all *acephalic*, without any indication of an external head skeleton (Fig. 39.10C).

Many Nematocera have distinct, segmented antennae, and most have normal, chewing mouth-parts, with the mandibles hinged to move in the horizontal plane. In some families, the labrum bears a pair of ventral appendage-like structures, the *premandibles*, which may take the form of toothed plates or processes (e.g. *Trichoceridae*, *Chironomidae*); or there may be paired, mobile, brush-like organs (the *mouth-brushes* or *cephalic fans* of *Culicidae*, *Simuliidae*, etc.; Figs 39.12G, 13F). Ventral to the mouth opening, there may be a median toothed plate, often called 'mentum' or 'submentum' (e.g. in *Culicidae*), but probably belonging to the head capsule proper. It is better termed the *hypostoma* (J. F. McAlpine *et al.* 1981). In the *Orthorrhapha*, the mandibles move in the vertical plane and are modified to sickle- or hook-like structures, whereas the maxillae, and sometimes antennae are fairly well developed. In the *Cyclorhapha*, the antennae are rudimentary and the mouth-parts and associated

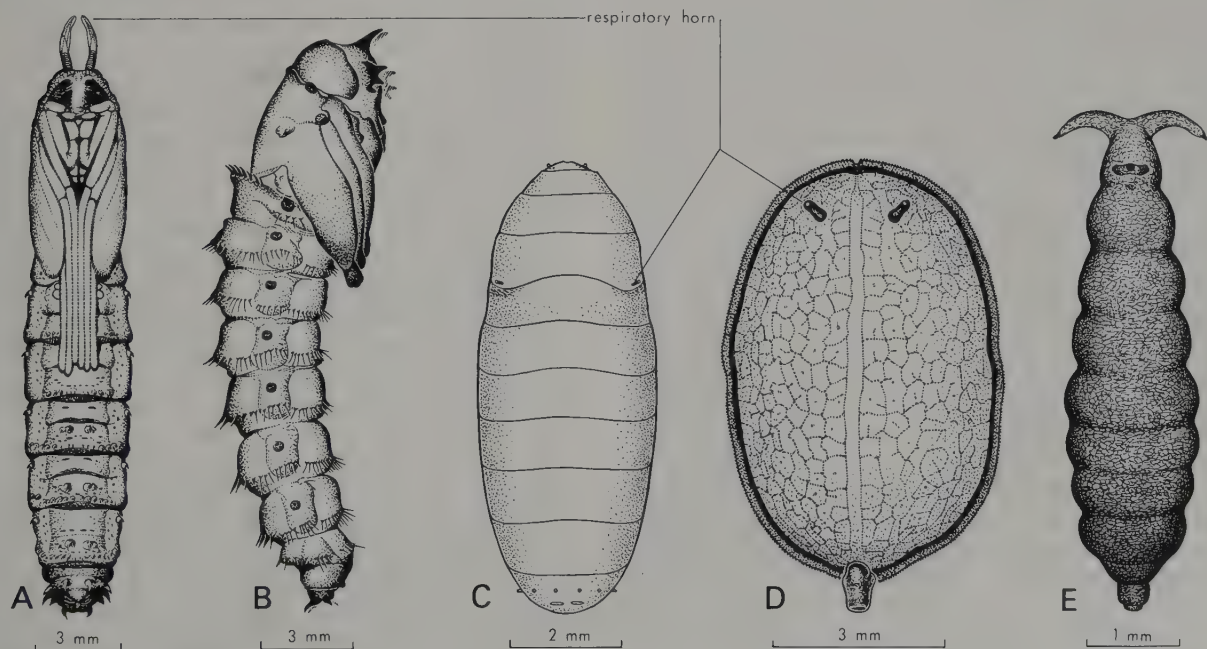


Fig. 39.11 Pupae and puparia: A, *Ischnotoma rubriventris*, Tipulidae, ventral; B, unidentified sp. of Asilidae, lateral; C, *Lucilia cuprina*, Calliphoridae, puparium; D, *Microdon* sp., Syrphidae, puparium; E, unidentified muscid, puparium. [T. Binder]



pharyngeal structures form a characteristic *cephalopharyngeal* skeleton (Fig. 39.10C). The principal parts are the paired, anterior *mouth-hooks* (mandibles) and the sclerotised areas of the pharynx: the latter usually as a pair of *pharyngeal plates*, each produced posteriorly into a *dorsal* and a *ventral cornu*.

Spiracles, functional or rudimentary, are present on the pro- and metathorax and 8 abdominal segments, the arrangement of *functional* spiracles varying considerably, usually between families, but also between instars of a single species (for details of spiracular structure, see J. F. McAlpine *et al.* 1981). Mature larvae of the more primitive families are often holopneustic (e.g. Bibionidae, Stratiomyidae), or peripneustic, lacking the metathoracic spiracle (e.g. Cecidomyiidae) or the posterior abdominal pair as well (e.g. Sciaridae). However, some are metapneustic (e.g. Culicidae, Tipulidae), amphipneustic (e.g. Anisopodidae), propneustic (e.g. some Mycetophilidae) or apneustic (e.g. most Chironomidae). With the exception of some Stratiomyidae, the Brachycera are typically amphipneustic. In all but the asiloid families, the posterior pair of spiracles tend to be approximated on the penultimate or ultimate segment; in some, they lie in a deep cleft or depression (Nemestrinidae, Sarcophagidae), at the apex of a breathing tube or *siphon* (Psychodidae, Culicidae—Figs 39.12F, H), or even on paired individual siphons (Scatopsidae—Fig. 39.14G). The siphon (e.g. in *Mansonia*, Culicidae) may be modified to take air from tissues of aquatic plants.

Internally, the alimentary canal is a relatively simple tube, though greatly convoluted in most Cyclorrhapha. The oesophagus projects into the mid gut, to form a valve or *cardia*, immediately behind which lies a series of enteric caeca; Cyclorrhapha may also have an oesophageal diverticulum, as in the adult. There are normally 4 or 5 Malpighian tubules. Salivary glands are always prominent, usually tubular and elongate, and sometimes very large (e.g. in *Mycetophila*). The nervous system tends to resemble that of the adult, the Nematocera with ganglia in most segments, the Cyclorrhapha with a single ganglionic mass. The brain may be in the head capsule, if present, or in the thorax. The tracheal system consists principally of 2 dorsal and 2 lateral longitudinal trunks, with a largely segmental series of dorsal anastomoses and lateral connectives; details of the pattern provide characters of considerable taxonomic and phylogenetic importance (Whitten 1963).

**Pupa** (Fig. 39.11). Dipterous pupae are usually immobile, though capable of rapid swimming movements in many Culicomorpha; the sluggish movement seen in many families is said to be that of the pharate adult. All are aedeicous, and in the Nematocera and Orthorrhapha almost all are obtect, the adhering sheaths of the legs and wings being termed *pedothecae* and *pterothecae*, respectively. The Cyclorrhapha are secondarily exarate and coarctate, with their delicate integument protected within a usually globular or barrel-shaped *puparium* (Fig. 39.11C). This is formed from the retained, hardened skin of the 3rd larval instar, and is lined with a delicate moulting membrane (Hinton 1958b). Functionally transitional

types of puparia have been independently evolved on several occasions. In Stratiomyidae and Perissommatidae, the delicate pupa, more or less exarate in the former but obtect in the latter, is enclosed within the unmodified last larval skin; in Scatopsidae, a normal, sclerotised, obtect pupa is almost completely enclosed in the last larval skin; and in a number of nematoceros pupae (e.g. some Tipulidae and Chironomidae), the larval skin remains attached to the posterior segments of the abdomen.

In many families the obtect pupa is enclosed in a silken cocoon, the walls often incorporating substrate materials. Such pupae may bear sharp anterior processes ('cocoon cutters'), while in all groups the integument often bears spines and tubercles that have various functions during eclosion of the adult. These furnish important taxonomic characters, as do the relative lengths and positions of the appendage sheaths; e.g. in Bibionidae, Psychodidae and several other families the pedothecae lie one above the other, instead of side by side.

Although functional spiracles may be present on the abdomen, most pupae respire mainly or entirely by the 'prothoracic' pair (as in the larva, actually mesothoracic spiracles that have migrated forward). These may be sessile, but frequently bear long, projecting extensions, the *respiratory horns* or *trumpets* (Fig. 39.11), which, although usually more or less rod-like, may be filamentous and branched. In aquatic forms, they may act as gills, operating via a plastron (e.g. Hinton 1962), or, as in the larvae, may take air from plant tissues. In the coarctate pupae of the Cyclorrhapha, most acalyptrates have the prothoracic spiracles internal, enclosed within the puparium; most other Cyclorrhapha have, in addition to the internal spiracles, a pair of respiratory horns formed by extensions of the spiracular chambers. These, in a most remarkable fashion, come to penetrate, and protrude through, special thin 'windows' in the first abdominal segment of the puparium (Keilin 1944; Roddy 1955).

## Biology

**Adults.** Adult Diptera are free living and ubiquitous. They are found in aerial plankton and in practically all terrestrial habitats: females of the extraordinary chironomid *Pontomyia* even spend some time submerged beneath the sea. At least some families form significant elements of the fauna in desert regions, intertidal zones, rainforests and snowfields. Their often considerable powers of flight make them generally wide ranging within broadly defined habitats, although some are more restricted, e.g. the ectoparasites that live mainly on the host's skin. Generally, the majority of species are associated with forest or water.

Except for a few groups with non-functional mouthparts (e.g. Oestridae), most adults are polyphagous. They take mainly the liquid food for which their mouth-parts are specially adapted although at least some Syrphidae and Empididae also eat pollen (Holloway 1976; Downes and Smith 1969). Such liquids include free water; a variety of animal and plant secretions; products of decomposition of organic matter; soluble solids, which are first liquefied by salivary secretions; and the tissue



fluids of other animals. The last refers to the large and important group which preys upon, or parasitises, other arthropods and vertebrates. Most of these species extract the host's body fluids by inserting a sharp proboscis, although the Dolichopodidae and Ephydriidae, for instance, 'masticate' their prey between their labella, while some Cyclorrhapha merely lacerate the skin with their prestomal teeth and suck up the exuding fluids.

Downes and Dahlem (1987) suggest that honeydew from Hemiptera was the primitive energy source for Diptera and that, inter alia, the pseudotracheate labellum originated as an adaptation for obtaining sugars from honeydew.

**Reproduction.** Almost all Diptera are normally bisexual; parthenogenesis is rare (e.g. in certain Psychodidae, Chironomidae), while paedogenesis occurs in some Cecidomyiidae. Except in the acalyptrate Schizophora, mating commonly takes place, or at least may continue, on the wing, and pairs are sometimes captured *in copula*. In some groups, particularly in Nematocera, it is usually preceded by formation of dancing swarms of males, while various forms of elaborate courtship procedure occur in the Empididae (Melander 1927) and other families. The female may be inseminated periodically by a number of males, but in some species she mates only once in her lifetime. Peacock and Erickson (1965) demonstrated that in *Drosophila melanogaster* half of the spermatozoa are regularly non-functional, and the phenomenon may well be present in other families. Sex ratios are usually normal, but *Chrysomya rufifacies* (Calliphoridae) is exceptional, in that individual females produce either all male, or all female, offspring throughout their lives (Norris, in Keast *et al.* 1959). This phenomenon, of 'unisexual families', is also common amongst the Cecidomyiidae (e.g. H. F. Barnes 1949) and probably occurs in some Australian Sciaridae (Metz 1938).

Development of the ova is usually rapid, being complete in a matter of days after eclosion (or minutes in the chironomid *Polypedium nubifer*), and may be independent of insemination. It may, however, require a prior meal of protein (some Calliphoridae) or blood (*anautogenous*, as opposed to *autogenous*, Culicidae). The eggs (or larvae) are deposited in, on, or near a substrate suitable for larval development, the gravid female being quite precisely guided by physical and chemical stimuli from the environment. Some Cyclorrhapha are *ovolarviparous*, the egg hatching immediately after deposition or *larviparous* (ovoviviparous), hatching in the oviduct before deposition; in *macrolarviparous* species (e.g. Amaniinae), a substantial amount of larval development takes place in the oviduct (uterus), with associated adaptations in anatomy and physiology (Ferrar 1978). The 'pupiparous' families (Hippoboscidae, Streblidae and Nycteribiidae) and the African *Glossina* (tsetse flies) show the highly evolved condition of *adenotrophic viviparity*, in which the larva develops in the uterus, feeding on secretions from maternal 'milk-glands'; it grows to full size and pupates soon after deposition. In many, if not most, Diptera, the maturation and release of the eggs leave visible traces, such as stretching of the ovarian tracheae or

oviduct, or *follicular relics* within the ovarioles. These have made possible a number of very useful techniques for age determination (Tyndale-Biscoe 1984).

**Immature Stages.** Dipterous eggs usually hatch fairly rapidly—diapause is known in some groups, but seems to be uncommon. Larval habitats are usually in moist situations: in mud, soil, etc.; in decomposing organic matter; in plant or animal tissues; or in free water. Apart from parasitic forms, most larvae crawl or swim actively in the breeding medium, although those of the Simuliidae and Blephariceridae are more sedentary, and live anchored to stones and other objects in flowing water; also, many aquatic Chironomidae inhabit small silken tubes in bottom silt or attached to debris. Some larvae are predators or parasites, devouring the tissues and/or body fluids of their hosts, whereas the remainder feed on fragments of organic matter. Noteworthy amongst feeding devices are the mouth-brushes of Culicidae and Simuliidae, which strain food particles from the surrounding water; the aquatic Stratiomyidae appear to have an analogous, but not homologous, organ.

Larval respiration is commonly direct from the atmosphere, even in liquid media. Many aquatic forms surface for air, though a few (e.g. in Culicidae, Tipulidae and Syrphidae) take air from plant tissues; others (particularly Chironomidae, Simuliidae and Ceratopogonidae) absorb dissolved oxygen directly from the water, a process assisted in certain bottom-dwelling Chironomidae by the presence of haemoglobin in their blood. The endoparasitic larvae form an analogous series. Many take air through perforations in the host's integument or tracheae (e.g. Tachinidae); others use air in plant tissues (e.g. leaf-miners); while yet others draw directly on oxygen dissolved in the host's blood (e.g. early stages of various families).

Pupation may occur in the larval breeding medium (e.g. in most aquatic forms and soil-dwellers), but in many families, both free living and parasitic, the mature larvae leave their very moist habitat to pupate in relatively drier sites near by, usually in the soil. This applies even to some aquatic forms (e.g. Tipulidae). The cyclorrhaphous pupae (and a few others) are protected within puparia, while many Nematocera (e.g. Simuliidae, Mycetophilidae) spin silken cocoons. Before eclosion, obtect 'pupae' (pharate adults) may first wriggle free from any surrounding cocoon (or puparium in Perissommatidae). Aquatic forms commonly come to the surface (e.g. Chironomidae), but adult Simuliidae emerge from the pupal shell *in situ*, beneath the surface.

The pharate adult bursts from the pupal skin or puparium usually by the pressure of swallowed air. In obtect pupae, it emerges from a longitudinal slit on the pupal thorax and sometimes abdomen. In coarctate forms, the anterior end of the puparium is pushed off or open, and the pushing process is facilitated by the *ptilinum*, a balloon-like sac of elastic cuticle, which can be protruded from above the bases of the antennae. Although the ptilinum is a characteristic feature of the Schizophora, at least some Aschiza (e.g. Syrphidae) have an analogous elasticity of the frontal cuticle that seems to function in



the same way. The processes of pupation and eclosion are reviewed by Hinton (1946b) and Fraenkel and Bhaskaran (1973).

**Natural Enemies.** Diptera, like most insects, are attacked by a wide range of predatory animals. Bats, birds, reptiles, Amphibia, dragonflies and spiders consume large numbers of adults, particularly of 'swarming' species, while sphecid wasps use them to provision their nurseries. Fishes, birds (to some extent), Odonata, Coleoptera and Hemiptera may feed on larvae and pupae of aquatic Diptera, while both adults and immature stages are attacked by other Diptera—adult Empididae, Asilidae, Dolichopodidae, etc., and the predatory larvae of many families, e.g. Muscidae. Fish (*Gambusia* and other genera) have even been utilised as controlling agents for mosquito larvae.

Apart from such generalised predation, Diptera support a wide range of parasites. Their ectoparasites are mainly Acarina, particularly Hydrachnoidea, which are common on aquatic species but probably cause little mortality; also, epibiont algae, fungi and protozoans (such as *Vorticella* spp.) may cause mortality in aquatic larvae. Their endoparasites have been more thoroughly studied, because of their potential use in biological control; a brief outline of the principal groups is given below.

**VIRUSES.** Little investigated; 'Tipula Iridescent Virus' is an example.

**BACTERIA.** Also little investigated, though known to cause mortality in aquatic larvae. *Bacillus thuringiensis israelensis* is specific to Diptera and is being used increasingly for control of aquatic Nematocera.

**FUNGI.** A number of specialised parasites are known; e.g. *Empusa* spp. of Cyclorrhapha; *Coelomomyces* and *Culicinomyces* almost entirely in larval Culicidae; and Laboulbeniales on adult Brachycera.

**PROTOZOA.** Apart from commensal species, pathogenic flagellates, gregarines and Microsporida are known from larvae and, to a lesser extent, adults of aquatic species.

**HELMINTHS.** Mainly nematodes; mermithids are rather common in some Culicomorpha.

**INSECTA.** Hymenoptera: Mainly in larvae and pupae (occasionally in eggs) of Cyclorrhapha, though a few are known from Orthorrhapha and Nematocera (Stammer 1956). Several species have been tested as biological control agents, but only *Opius* spp. against the Qld fruit fly has shown any promise. A variety of small wasps are known from higher Diptera; Braconidae (*Opius* spp. and various Alysini) parasitise acalyptrate Schizophora, the Dacnusiini particularly in the leaf-mining Agromyzidae; while predatory syrphids are parasitised by an ichneumonid (*Diplazon* sp.) and several Encyrtidae. Hyperparasitic species of Trigonalysidae and Perilampidae are known from Tachinidae, and of Encyrtidae from Acroceridae. Diptera: Relatively few known, mainly Tachinidae and Bombyliidae.

**Economic Significance.** The Diptera outrank all other orders of insects in medical and veterinary importance. Blood-sucking species are directly responsible for the transmission of malaria, filariasis, leishmaniasis, trypanosomiasis (sleeping sickness) and a wide range of arboviruses, including yellow fever, dengue and various encephalitides (Doherty *et al.* 1973; Lee *et al.* 1980–89). Most of the vector species are mosquitoes, but others are found in the Simuliidae, Ceratopogonidae, Psychodidae (*Phlebotomus*), Glossinidae and Tabanidae. Similarly transmitted are various Protozoa, helminths and viruses that cause disease in domestic animals and birds; e.g. trypanosomiasis (surra) in horses, the blue-tongue virus of sheep, and the avian malaras. These diseases of humans and animals are mostly absent, or of limited importance, in Australia; but in some areas the bites of mosquitoes, sand flies, black flies, horse flies and buffalo flies can create significant problems through physiological side effects and economic effects on land use. Indeed, the buffalo fly (*Haematobia exigua*) is a major pest of horses and cattle in tropical Australia.

Apart from the biting flies, the bush fly (*Musca vetustissima*) is a familiar pest, while the house fly (*Musca domestica*) is a cosmopolitan vector of enteric diseases. Larvae of other Cyclorrhapha (principally Calliphoridae) infest the tissues of livestock and occasionally humans, producing a condition known as myiasis. 'Blowfly strike' of sheep by *Lucilia cuprina* costs Australian industry millions of dollars annually, and we live under the threat that *Chrysomya bezziana*, which causes a similar and very serious myiasis in cattle, may be introduced from Papua New Guinea. Of lesser importance are the 'bot flies' (Oestridae, Gasterophilidae), whose larvae are internal parasites of sheep, horses and kangaroos, and the ectoparasitic Hippoboscidae (e.g. the sheep ked).

Cultivated plants probably suffer less from dipterous pests in Australia than in many other countries, but the Qld and Mediterranean fruit flies (Tephritidae) are serious pests of fruit. Also, leaf-miners and stem-borers (Agromyzidae, Chloropidae, Muscidae etc.), although of little significance now, may yet increase in importance with the development of tropical agriculture in the north.

Against this record can be set the numerous examples of beneficial species. Various Diptera play at least a secondary role as pollinators, some with highly specialised behaviour, e.g. the ceratopogonid *Forcipomyia* spp., and several mycetophilids that pollinate certain ground orchids. The order has been little used in Australia for planned biological control, although introduced cecidomyiids are of some importance in combatting weeds, e.g. *Zeuxidiplosis giardi* on St John's wort and *Cystiphora schmidtii* on skeleton weed. There are also numerous native predators and parasites which play at least some part in checking the activities of potential or actual pests. The biting flies, particularly the mosquitoes, have been of use as vectors of the myxoma virus which so dramatically reduced Australia's rabbit plague (Fenner and Ratcliffe 1965); larvae of Tachinidae, Bombyliidae and Nemeritidae are endoparasites of other insects, including many pest species; larvae of some Syrphidae and adults



of Dolichopodidae, Empididae, Asilidae and others feed largely on arthropod prey; and the phytophagous larvae of Cecidomyiidae assist in keeping in check plants, such as *Hakea* spp., that have shown potential as pests when introduced abroad. Generally, this aspect of the ecology of our native Diptera has been little investigated.

Special Features of the Australian Fauna

The Australian dipterous fauna may be regarded as more or less 'normal' in size—its probable total of some 10 000–12 000 species is about 5% of the estimated world total, as is (approximately) the whole Australian insect fauna, and that figure also represents the proportion of habitable land (i.e. excluding Antarctica) provided by Australia. Most families occur here, those missing being mainly small and specialised, principally acalyptate Schizophora, of which some may yet be discovered (as were the Cypselosomatidae in 1964 and the Xenasteiidae in 1981). However, the absence of the Ptychopteridae is noteworthy. This ancient family occurs in all other regions of the world, and its absence poses an interesting problem in biogeography. The exceptionally rich fauna of families such as Apioceridae, Coelopidae and Pyrgotidae is also to be noted.

The zoogeography of the Australian fauna has been discussed most recently by Paramonov (in Keast *et al.* 1959), Gressitt (1961) and, to some extent, Hennig (1960). The accepted biogeographic provinces are reflected in the distributions of dipterous species, but the Eyrean is not very distinct, and is characterised mainly by the absence of groups found elsewhere. The most distinct elements of the fauna can be classified on the basis of their world distribution and probable origins, as follows.

(A) Taxa of obscure origin: (1) Endemic forms without obviously close relatives elsewhere, possibly relicts of ancient lineages; e.g. *Exeretonevra*. (2) Primitive forms with wide, but disjunct, world distributions, presumably relicts of an ancient fauna; e.g. *Nemopalpus* (Psychodidae), *Olbiogaster* (Anisopodidae). (3) Other forms with enigmatic distributions; e.g. *Enicoscolus* (Bibionidae), *Microphorella* (Empididae). (4) Cosmopolitan forms of such widespread distribution, perhaps by wind currents, that their origins are no longer discernible; e.g. various Chironomidae and Cecidomyiidae. The foregoing groups form a relatively small part of the fauna, and with increasing knowledge may yet be placed satisfactorily in the divisions below.

(B) Taxa showing evidence of probable origins: (1) 'Indo-Malayan' (northern); mostly recent, with close relatives in the Indo-Malayan subregion; they comprise numerous groups, particularly of Cyclorrhapha, principally Torresian in distribution, but with members penetrating throughout the continent. (2) 'Antarctic' (southern); almost all belonging to the Nematocera and Orthorrhapha, with near relatives in New Zealand, southern South America, and, in a few cases, South Africa; most are characteristically Bassian in distribution, but some penetrate well into the tropics, particularly at high altitudes. (3) Recent immigrants, including an apparent, and surprising, excess of Neotropical species; e.g. *Prosopeantrum flavifrons* (Heleomyzidae), *Fannia albitarsis* (Fanniidae), *Anthomyia punctipennis* (Anthomyiidae) and *Tricharaea brevicornis* (Sarcophagidae). Amongst the northern elements, some seem to have been derived from more ancient stocks than others, but the distinction is not clearly drawn. The southern element, found in so many floral and faunal groups, is very marked, and almost every family of Nematocera and Orthorrhapha offers examples of the 'Antarctic' distribution. In the Cyclorrhapha, the reverse is equally marked, and there are very few such groups.

The existence of the clear-cut 'Antarctic' elements is most satisfactorily explained by the theory of continental drift (Chapter 7), and it is relevant to note that the Tertiary fauna of the Northern Hemisphere seems to lack all the typically 'Antarctic' groups of Nematocera and Orthorrhapha (Colless 1964). Apparently, when Gondwana separated from Laurasia in about the Late Jurassic, the main stocks of the Nematocera and Orthorrhapha were already well established, along with the ancestors of the Aschiza. However, the Schizophora had not yet evolved, or at least were insufficiently widespread to gain a foothold on the Australian plate before it embarked on its long journey through southern latitudes. During that journey the characteristic 'Antarctic' fauna arose, by joint evolution over still-connected elements of Gondwana or differential extinction of ancient stocks in Laurasia. Probably both processes operated. Eventually the Australian plate came against the Sunda Shelf in about the Miocene, to begin a complex faunal exchange that may well be still operating. Possibly, Australia thereby gained almost all its Muscoidea, whole families such as Syrphidae and (perhaps) Culicidae, and genera such as *Epicrypta* (Mycetophilidae). What it may have given in return remains unclear.

CLASSIFICATION

Order DIPTERA  
(7786 Australian spp.)

Suborder NEMATOCERA (2107)

Division NYMPHOMYIOMORPHA (0)  
Nymphomyiidae (0)

Division TIPULOMORPHA (710)  
1. Tipulidae (704)  
2. Trichoceridae (6)

## Division TANYDEROMORPHA (6)

3. Tanyderidae (6)

## Division PTYCHOPTEROMORPHA (0)

- Ptychopteridae (0)

## Division BLEPHARICEROMORPHA (25)

4. Blephariceridae (25)

- Deuterophlebiidae (0)

## Division CULICOMORPHA (731)

## CULICOIDEA (296)

5. Chaoboridae (10)  
6. Dixidae (11)  
7. Culicidae (275)

## CHIRONOMOIDEA (435)

8. Chironomidae (202)  
9. Ceratopogonidae (174)

10. Simuliidae (38)  
11. Thaumaleidae (21)

## Division PSYCHODOMORPHA (115)

12. Psychodidae (115)

## Division BIBIONOMORPHA (520)

13. Anisopodidae (4)  
Pachyneuridae (0)  
Axymyiidae (0)  
14. Perissomatidae (4)

15. Scatopsidae (57)  
Synneuridae (0)  
Canthyloscelidae (0)  
16. Bibionidae (32)

17. Cecidomyiidae (112)  
18. Sciaridae (61)  
19. Mycetophilidae (250)

## Suborder BRACHYCERA (5679)

## Division ORTHORRHAPHA (2270)

## TABANOIDEA (526)

20. Pelecorhynchidae (34)  
21. Rhagionidae (54)  
22. Athericidae (12)  
Vermileonidae (0)  
23. Tabanidae (243)  
Pantophthalmidae (0)  
24. Stratiomyidae (92)

25. Xylomyidae (1)  
26. Xylophagidae (4)  
27. Nemestrinidae (52)  
28. Acroceridae (34)

31. Asilidae (640)  
32. Apioceridae (75)  
33. Mydidae (35)  
34. Bombyliidae (391)

## ASILOIDEA (1336)

29. Therevidae (112)  
30. Scenopinidae (83)

## EMPIDOIDEA (408)

35. Empididae (88)  
36. Dolichopodidae (320)

## Division CYCLORRHAPHA (3409)

## Series ASCHIZA (304)

## LONCHOPTEROIDEA (1)

37. Lonchopteridae (1)

## PHOROIDEA (104)

38. Ironomyiidae (2)

39. Platypezidae (11)  
40. Sciadoceridae (1)  
41. Phoridae (90)

## SYRPHOIDEA (199)

42. Pipunculidae (30)  
43. Syrphidae (169)

## Series SCHIZOPHORA (3105)

## CONOPOIDEA (75)

44. Conopidae (75)

## SCIOMYZOIDEA (425)

- Dryomyzidae (0)  
Helcomyzidae (0)  
45. Sciomyzidae (11)  
Huttoninidae (0)  
46. Helosciomyzidae (8)  
47. Coelopidae (11)  
Ropalomeridae (0)  
48. Sepsidae (16)  
Eurychoromyiidae (0)  
49. Chamaemyiidae (12)  
50. Lauxaniidae (367)

## DIOPSOIDEA (5)

- Diopsidae (0)  
Syringogastridae (0)  
Nothybidae (0)  
51. Tanypezidae (3)  
52. Psilidae (2)  
Somatiidae (0)

## TEPHRITOIDEA (503)

53. Lonchaeidae (21)  
54. Piophilidae (7)  
Pallopteridae (0)  
Richardiidae (0)  
55. Otitidae (4)  
56. Platystomatidae (236)  
57. Pyrgotidae (100)  
58. Tephritidae (135)  
Tachiniscidae (0)  
Ctenostylidae (0)

## NERIOIDEA (24)

59. Pseudopomyzidae (1)  
60. Cypselosomatidae (3)  
61. Neriidae (2)  
Megamerinidae (0)

## HELEOMYZOIDEA (130)

62. Micropezidae (18)  
63. Heleomyzidae (67)  
64. Sphaeroceridae (60)  
65. Chyromyidae (3)

## OPOMYZOIDEA (210)

- Opomyzidae (0)  
66. Clusiidae (29)  
Acartophthalmidae (0)  
67. Odiinidae (3)  
68. Agromyzidae (150)  
69. Fergusoninidae (25)  
70. Xenasteiidae (2)  
71. Carnidae (1)

## ASTEIOIDEA (54)

72. Neurochaetidae (3)  
73. Periscelididae (13)  
74. Teratomyzidae (24)  
75. Aulacigastridae (7)  
76. Asteiidae (6)  
77. Anthomyzidae (1)

## EPHYDROIDEA (337)

- Campichoetidae (0)  
Diastatidae (0)  
78. Ephydriidae (85)  
Camillidae (0)



79. Curtonotidae (1)	MUSCOIDEA (1008)	92. unnamed family (12)
80. Drosophilidae (247)	Scathophagidae (0)	93. Tachinidae (542)
81. Cryptochetidae (4)	Mormotomiidae (0)	Rhinophoridae (0)
CHLOROPOIDEA (333)	87. Anthomyiidae (9)	94. Gasterophilidae (3)
82. Tethinidae (8)	88. Fanniidae (11)	95. Oestridae (3)
83. Canacidae (9)	89. Muscidae (180)	Glossinidae (0)
84. Milichiidae (16)	90. Calliphoridae (140)	96. Hippoboscidae (30)
85. Chloropidae (300)	91. Sarcophagidae (67)	97. Streblidae (7)
BRAULOIDEA (1)	Mystacinobiidae (0)	98. Nycteribiidae (16)
86. Braulidae (1)		

Since the 1st edition of this book, there have been several major revisions of the classification of Diptera (e.g. Hennig 1973; J. F. McAlpine *et al.* 1981–89) and we are aware of others in preparation or in press. The frequency and extent of these revisions warn against accepting any one of them as definitive, especially in a regional textbook where continuity is important. There are also the problems of dogmatic cladism; for instance, we remain unconvinced that a paraphyletic taxon cannot be a perfectly good one. Especially, we see it as no reason for the fragmentation of traditional, ‘good’ families such as the Empididae and Mycetophilidae.

We have employed here a classification that to a large extent follows our original. However, the classification within the acalyptrate Schizophora has been extensively reworked, following the studies of the second author; and the number of ‘Divisions’ in Nematocera has been increased from four to eight, four of them monotypic. The latter change reflects the views of the first author that, for instance, to group Nymphomyiidae with any other family

yields a singularly uninformative taxon, of very doubtful utility. Indeed, much the same could be said of the groupings conserved under Tipulomorpha and Blephariceromorpha. Similarly, we have acknowledged the clear-cut superfamilies available in Culicomorpha, but have avoided that category in Bibionomorpha, where the only convincing cluster is that comprising Mycetophilidae, Sciaridae and (perhaps) Cecidomyiidae. In cases of conflict such as the well-known similarity of larvae of Trichoceridae, Anisopodidae, Psychodidae and Scatopsidae, which yields groupings highly incongruent with those based on adult characters, we have taken a conservative stance. There, and elsewhere, we can only hope that the currently accelerating accrual of new information (e.g. Shaw and Meinertzhagen 1986) will eventually lead to convincing solutions.

The keys have been designed primarily for convenience in identification and make no pretence to be ‘natural’. For this reason, the Cyclorrhapha Aschiza have been included in a single key with the Orthorrhapha.

KEYS TO THE MAJOR GROUPS OF DIPTERA

ADULTS

- 1. Antenna relatively simple, often filiform, and longer than thorax, with scape, pedicel and a flagellum of 6–14 segments, rarely more or less (Figs 39.2A–F); maxillary palps usually with 3–5 segments (rarely reduced); vein CuA rarely converging towards 1A (except in Bibionidae), never meeting it; discal cell often absent; mesopleural suture following a roughly straight or wavy line from wing root to mid coxa (except in some Psychodidae and Scatopsidae). Mostly rather slender flies ..... NEMATOCERA (p. 736)
- Antenna usually short, with less than 7 segments (except in some Orthorrhapha), often highly modified, terminating in a narrow style or bristle-like arista (Figs 39.2G–K); maxillary palps with 1 or 2 segments; vein CuA converging towards 1A, often meeting it; discal cell usually present; mesopleural suture sharply angled where it meets sternopleuron, and often similarly angled posteriorly around that sclerite. Often more stoutly built flies ..... BRACHYCERA. 2
- 2(1). Ptilinal fissure absent, the sutures, if any, at sides of face not confluent above antennae (except in a few Syrphidae); R<sub>4+5</sub> sometimes branched; CuA often long, reaching wing margin or joining 1A near its apex ..... Orthorrhapha (p. 751) and Cyclorrhapha-Aschiza (p. 761)
- Ptilinal fissure present above bases of antennae, continuing down sides of face as an inverted U; R<sub>4+5</sub> unbranched; CuA usually short and joining 1A well back from its apex, usually towards its base ..... Cyclorrhapha-Schizophora (p. 763)

MATURE LARVAE

- 1. Head capsule usually well formed, complete, or with deep incisions posteriorly (may be considerably reduced or modified in Cecidomyiidae, Tipulidae and Blephariceridae); mandibles usually of chewing type, toothed, opposable and moving in horizontal plane of head (Fig. 39.10A) ..... NEMATOCERA (p. 736)
- Head capsule absent or incomplete posteriorly; if incomplete, then with a strong internal skeleton of usually paired rods retracted within the thorax; mandibles usually hook- or sickle-shaped, moving in the vertical plane of head ..... BRACHYCERA. 2
- 2(1). Head capsule partially developed, more or less retracted within prothorax, the anterior portion with a distinct dorsal sclerite, which bears the usually well-formed antennae; posterior portion with an internal skeleton of longitudinal rods; mandibles usually sickle shaped, not attached to a cephalopharyngeal skeleton (Fig. 39.10B) .... Orthorrhapha (p. 751)
- Head capsule not developed, without dorsal sclerotisation; antennae absent, or poorly developed, borne on membranous areas; mandibles replaced by ‘mouth-hooks’, attached to a characteristic cephalopharyngeal skeleton (Fig. 39.10C) ..... Cyclorrhapha (p. 761)

### Suborder NEMATOCERA

Mostly small, rather delicate flies, with the general characteristics given in the key; also with X and Y chromosomes not forming bivalents at spermatogenesis (except in Ptychopteridae), or sex-chromosomes apparently absent.

Generally, the Nematocera most closely resemble the hypothesised ancestral Diptera and include the oldest families, some known from Jurassic fossils. Some, e.g. the Culicidae, show considerable specialisation, and have probably undergone relatively recent radiations.

#### *Keys to the Families of Nematocera Known in Australia*

#### ADULTS

1. Wings with a secondary network of vein-like markings; slender, long-legged flies (Figs 39.18B, C) ..... **Blephariceridae** (p. 742)
- Wings without such markings ..... 2
- 2(1). Discal cell and ocelli both present ..... 3
- Discal cell and/or ocelli absent ..... 5
- 3(2).  $R_{2+3}$  forked,  $R_2$  ending in costa; eyes divided laterally into completely separated dorsal and ventral components; small flies (Figs 39.18D, E) ..... **Perissommatidae** (p. 747)
- $R_2$  absent, or ending in  $R_1$ ; eyes normal, at most differentiated into contiguous areas of different facet size ..... 4
- 4(3). Delicate, long-legged flies; mesonotum with V-shaped transverse suture; 2A short but strong, curved down to meet wing margin (Fig. 39.7B) ..... **Trichoceridae\*** (p. 742)
- Stoutly built flies; mesonotum without such suture; 2A weak, not reaching wing margin (Fig. 39.18A) ..... **Anisopodidae** (p. 747)
- 5(2). Mesonotum with complete V-shaped transverse suture; wing with 2 complete anal veins reaching margin; long-legged flies (Fig. 39.15) ..... **Tipulidae\*** (p. 740)
- Mesonotum without V-shaped suture (indicated, but incomplete centrally in Tanyderidae); wing with at most a single complete anal vein reaching margin ..... 6
- 6(5). Discal cell present; rather large, long-legged flies, with patterned wings (Fig. 39.16A) ..... **Tanyderidae** (p. 742)
- Discal cell absent ..... 7
- 7(6). Small to minute, delicate flies, often with elongate, moniliform antennae; wings usually hairy, with Rs unbranched, few main veins, and few or no cross-veins; eyes bridged above the antennal sockets; tibiae without spurs; coxae usually not elongate (Fig. 39.20E) ..... **Cecidomyiidae** (p. 749)
- Not with the above combination of characters ..... 8
- 8(7). Ocelli present ..... 9
- Ocelli absent ..... 13
- 9(8). Mid and hind tibiae with 1 or 2 distinct apical spurs; radial veins not conspicuously stronger than others ..... 10
- Mid and hind tibiae without apical spurs; radial veins very strong, other veins much weaker (Fig. 39.19B) ..... **Scatopsidae** (p. 747)
- 10(9). Antennae arising from near or below level of lower margins of eyes; empodium and pulvilli strongly and equally developed, forming a triple pad beneath the tarsal claws; coxae normal (Fig. 39.19A) ..... **Bibionidae** (p. 748)
- Antennae arising from near or above level of centre of eyes; pulvilli at most weakly developed; coxae more or less elongate ..... 11
- 11(10). Eyes usually connected dorsally above the antennae; a distinct midpleural pit usually present below the wing-root; wing with characteristic venation,  $r-m$  in line with apical portion of Rs,  $M_{3+4}$  arising near base of wing; tibiae without strong spines (Figs 39.20C, D) ..... **Sciaridae** (p. 749)
- Eyes not connected dorsally; midpleural pit indistinct or absent; wing venation not as above, and/or tibiae with strong spines (Figs 39.20A, B) ..... **Mycetophilidae** (p. 749)
- 12(8). Wings broadly ovate, often pointed; M always 4-branched, Rs sometimes 4-branched, cross-veins usually restricted to basal third of wing; mostly small, very hairy, moth-like flies (Fig. 39.16B) ..... **Psychodidae** (p. 747)
- Both M and Rs with 3 or fewer branches ..... 13
- 13(12). Rs and M each with 3 branches ..... 14
- R<sub>s</sub>, and/or M, with fewer than 3 branches ..... 16
- 14(13).  $R_{2+3}$  strongly arched, not in line with main stem of Rs; wing veins with sparse setulae; mouth-parts not forming an elongate proboscis (Fig. 39.17H) ..... **Dixidae** (p. 743)
- $R_{2+3}$  not arched, more or less in line with main stem of Rs; wing veins clothed with abundant hairs or scales; most species with mouth-parts forming an elongate proboscis (Figs 39.17C, D) ..... 15
- 15(14). Proboscis long, extending well beyond clypeus; head, legs and (usually) abdomen clad with scales ..... **Culicidae** (p. 743)
- Proboscis short, barely extending beyond clypeus; body clad with hairs only ..... **Chaoboridae** (p. 742)
- 16(13).  $R_2$  short, vertical;  $R_3$  distinctly arched on its basal half; antennae short in both sexes, apical part of flagellum abruptly narrowed, fine (Fig. 39.17F) ..... **Thaumaleidae** (p. 747)
- Radial veins and antennae otherwise;  $R_2$  usually vestigial or absent ..... 17

\* Shriveled specimens of Trichoceridae, in which the ocelli may be overlooked, will key to Tipulidae, but may be recognised by the very short, curved 2A.



- 17(16). Wings very broad, with large anal lobe;  $M_{3+4}$  arising at extreme base of wing; small, stout, biting flies (Fig. 39.17E) ..... **Simuliidae** (p. 746)  
Wings mostly longer and narrower, with small anal lobe or none;  $M_{3+4}$  forking from CuA at about centre of wing ..... 18
- 18(17).  $M_1$  and  $M_2$  both present; radial veins short, usually meeting costa well before apex of wing, and enclosing 1 or 2 radial cells; mouth-parts of piercing type (Fig. 39.17G) ..... **Ceratopogonidae** (p. 746)  
 $M_{1+2}$  unbranched, radial veins almost always longer,  $R_{4+5}$  almost always ending near apex of wing; mouth-parts almost always non-piercing (Figs 39.17A, B) ..... **Chironomidae** (p. 744)

MATURE LARVAE

1. Very small larvae, with 13 postcephalic segments and a tiny, much reduced head capsule; mouth-parts rudimentary; antennae distinct; mature larvae usually with a longitudinal sclerotised strip ('sternal spatula') ventrally on prothorax; peripneustic; terrestrial or in plant galls (Fig. 39.14H) ..... **Cecidomyiidae** (p. 749)  
Not with the above combination of characters ..... 2
- 2(1). Thorax, first 2 abdominal segments, and sometimes head capsule fused into a single large mass; the 5 or 6 apparent segments of abdomen separated by deep constrictions; ventrally with a conspicuous median row of sucking discs; attached to rocks, etc., in running water (Fig. 39.14A) ..... **Blephariceridae** (p. 742)

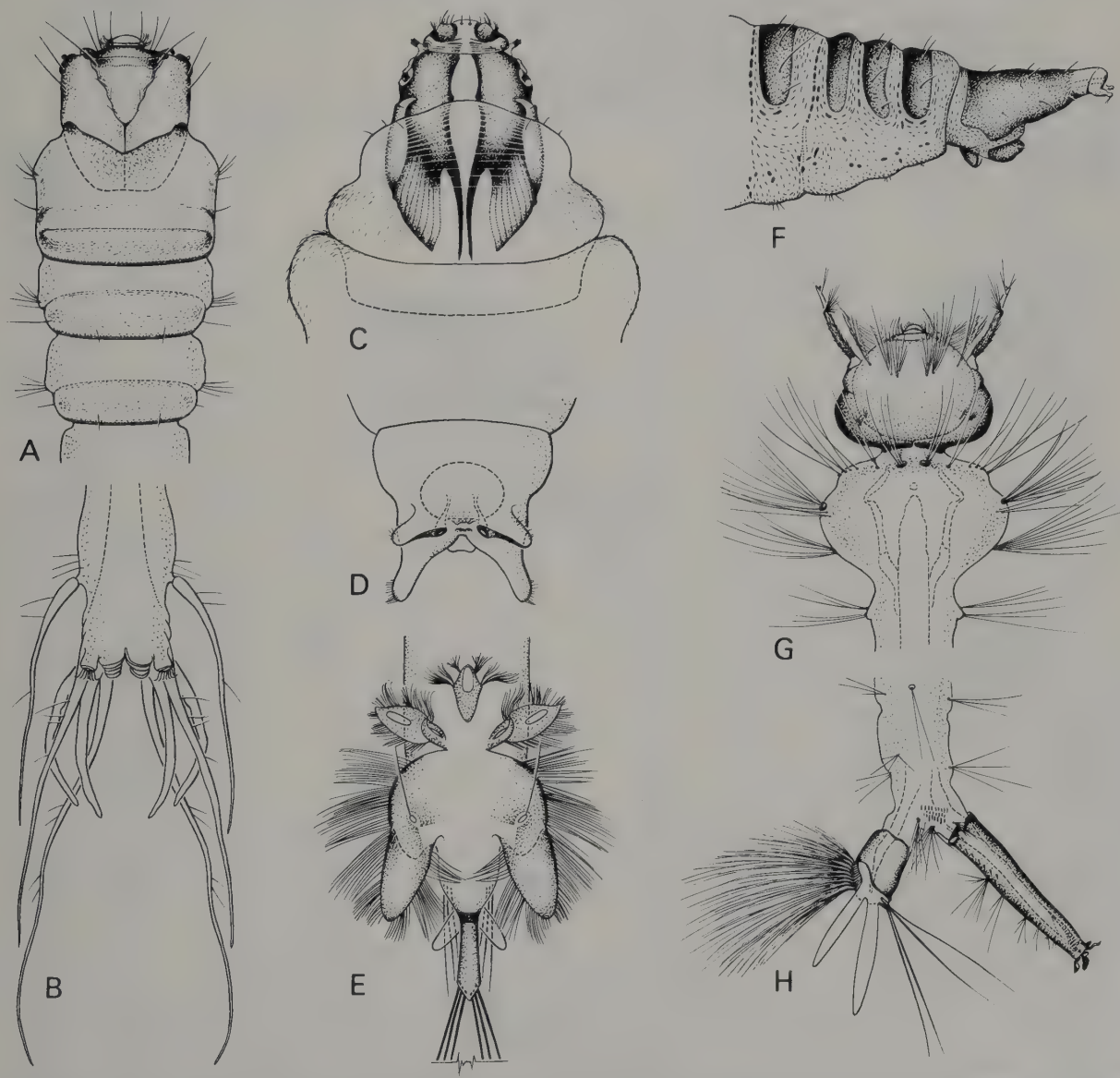


Fig. 39.12 Larvae of Nematocera (F and H lateral, remainder dorsal): A, *Eutanyderus wilsoni*, Tanyderidae, head and thorax; B, same, end of abdomen; C, *Dolichopeza* sp., Tipulidae, head and prothorax; D, *Trichocera annulata*, Trichoceridae, end of abdomen; E, *Dixia nicholsoni*, Dixidae, end of abdomen; F, unidentified sp. of Psychodidae, end of abdomen; G, *Culex australicus*, Culicidae, head and thorax (minor setae omitted); H, same, end of abdomen. [T. Binder]

- Not with the above combination of characters ..... 3
- 3(2). Head more or less retracted within thorax, sometimes completely so, capsule with the strongly sclerotised areas deeply incised posteriorly, or even reduced to little more than a series of longitudinal rods and plates; apex of abdomen often with radiating protuberances; terrestrial or aquatic (Fig. 39.12c) ..... **Tipulidae** (p. 740)
- Head capsule well formed, completely sclerotised dorsally, more or less exerted ..... 4
- 4(3). Abdomen with a club-like shape produced by dilated posterior segments, the apical segment encircled by a band composed of series of tiny hooks; thorax with a median ventral proleg; mouth-brushes (if present) conspicuous, fan-like; attached to submerged objects in running water (Fig. 39.13f) ..... **Simuliidae** (p. 746)
- Not with the above combination of characters ..... 5
- 5(4). Thorax with segments indistinctly differentiated, forming a single dilated mass; usually metapneustic, with posterior spiracles at apex of a sclerotised siphon or approximated on a complex dorsal plate; head large, highly mobile; aquatic, very active (Figs 39.12g, h) ..... 6
- Thorax with distinct segmentation ..... 7
- 6(5). Prominent mouth-brush of setae present on either side of labrum; antennae well separated, with short apical setae; abdomen without tracheal sacs ..... **Culicidae** (p. 743)
- Mouth-brushes absent, or borne on maxillae; antennae with conspicuous apical setae, half or more the length of shaft, and/or antenna bases approximated, and/or with tracheal sacs in thorax and abdomen ..... **Chaoboridae** (p. 742)

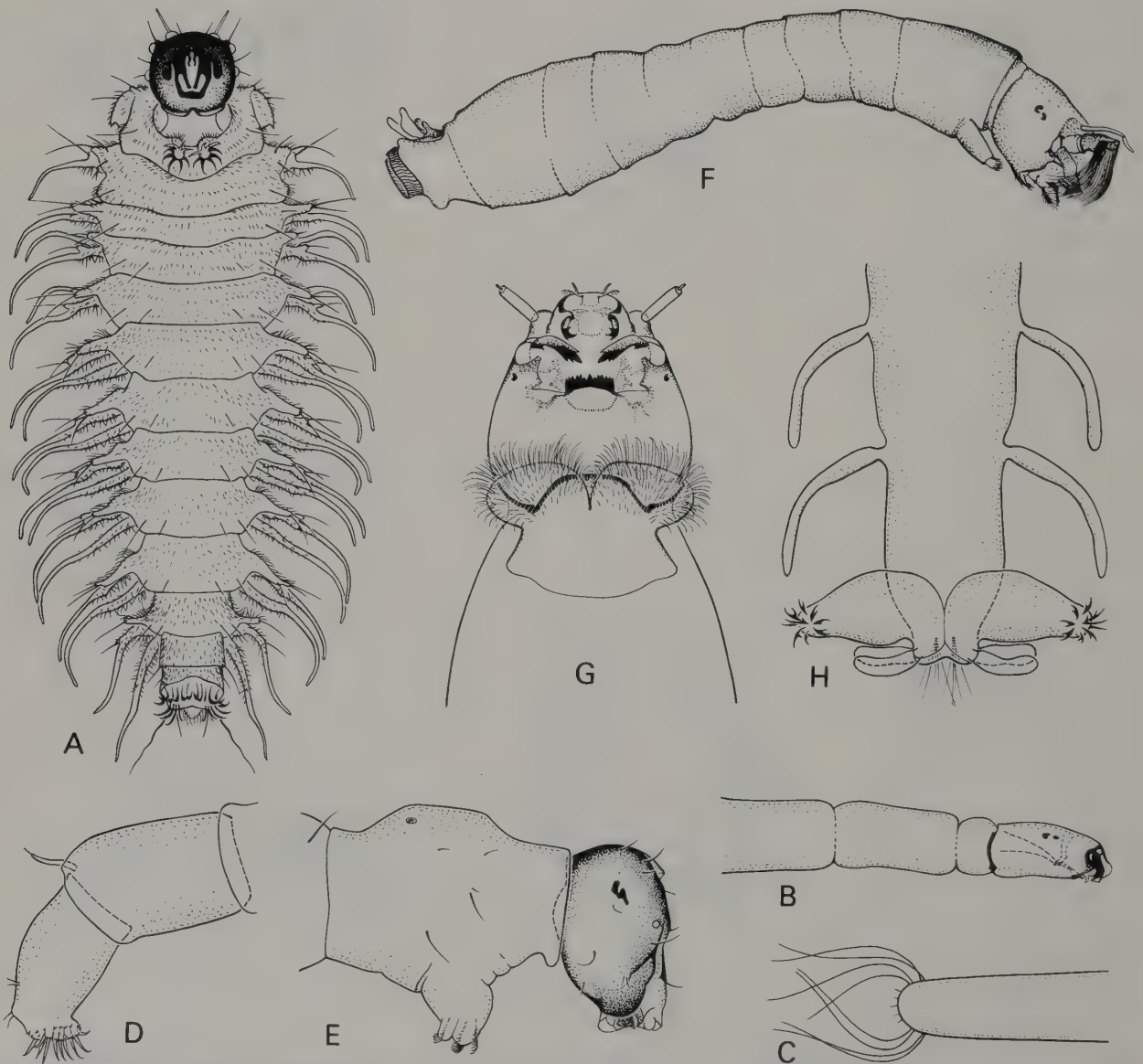


Fig. 39.13 Larvae of Nematocera: A, *Atrichopogon* sp., Ceratopogonidae, ventral; B, *Culicoides angularis*, Ceratopogonidae, head and thorax; C, same, apex of abdomen, lateral; D, *Austrothaumalea* sp., Thaumaleidae, apex of abdomen, lateral; E, same, head and thorax; F, *Simulium ornatipes*, Simuliidae; G, *Chironomus tepperi*, Chironomidae, head and thorax, ventral; H, same, apex of abdomen, ventral.

[T. Binder]



- 7(5). Abdominal segments 1 and 2 each with a pair of prolegs, which bear apical rows of short, curved, bristles; apex of abdomen with a pair of projecting plates fringed with long hairs and a short rod tipped with long bristles; aquatic (Fig. 39.12E) ..... **Dixidae** (p. 743)  
 Abdominal segments 1 and 2 without paired prolegs ..... 8
- 8(7). Peripneustic, the posterior spiracles borne on a pair of short, tubular, sclerotised siphons; small, terrestrial larvae (Fig. 39.14G) ..... **Scatopsidae** (p. 747)  
 Posterior spiracles, if present, sessile or borne on a single siphon ..... 9
- 9(8). Small larvae, completely sclerotised when mature; segmentation very distinct, simple; peripneustic, the posterior spiracles borne on a short, stout, tapering siphon; antennae rudimentary; head capsule indented laterally, not smoothly rounded; terrestrial (Fig. 39.14F) ..... **Perissommatidae** (p. 747)  
 Not with the above combination of characters ..... 10
- 10(9). Small larvae; amphipneustic or metapneustic; body with marked secondary segmentation, indicated on at least some segments by narrow, transverse, sclerotised strips; and/or posterior spiracles borne on a short, stout, tapering siphon; or apex of abdomen with several very long hairs (*Phlebotomus*); or 'louse-like' larvae, flattened, with long, 4-segmented antennae and dorsal plates fringed with fine processes (*Sycorax*); terrestrial or semiaquatic (Fig. 39.12F) ..... **Psychodidae** (p. 747)

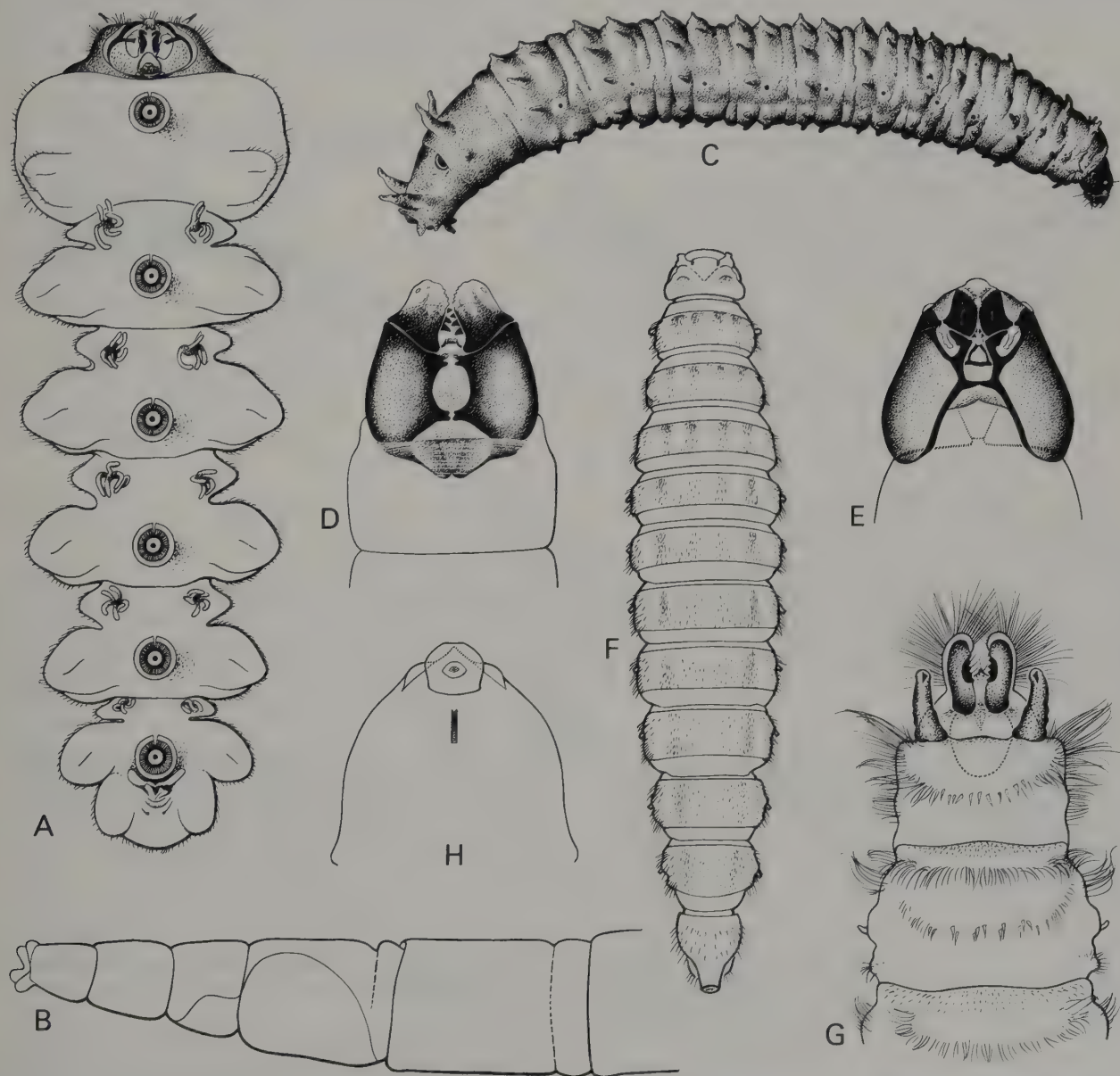


Fig. 39.14 Larvae of Nematocera: A, *Edwardsina ferrugiana*, Blephariceridae, ventral; B, *Sylvicola dubius*, Anisopodidae, apex of abdomen, lateral; C, unidentified sp. of Bibionidae; D, *Sciara* sp., Sciariidae, head, ventral; E, *Exechia* sp., Mycetophilidae, head, ventral; F, *Perissomma fusca*, Perissommatidae, dorsal; G, *Scatopse fuscipes*, Scatopsidae, apex of abdomen, dorsal; H, *Zeuxidiplosis giardi*, Cecidomyiidae, head and thorax, ventral. [T. Binder]

- Not with the above combination of characters ..... 11
- 11(10). Head projecting ventrally, at about a right angle to thorax, with short hairs and/or knob-like protuberances; antennae rudimentary; prothorax with median pseudopod ventrally; apex of abdomen with semicircle or cluster of hooklets; amphipneustic, thoracic spiracles distinct; aquatic (Figs 39.13D, E) ..... **Thaumaleidae** (p. 747)
- Not with the above combination of characters ..... 12
- 12(11). Apneustic; often with prolegs, bearing apical spines or hooklets, on prothorax and sometimes on apex of abdomen also; aquatic ..... 13
- Spiracles distinct on at least prothorax and apex of abdomen; prolegs absent; terrestrial ..... 15
- 13(12). Anterior margin of head truncate, almost rectangular; thorax and abdomen with a dorsal and a ventral protuberance ('creeping welts') on most segments; apex of abdomen with 8 long gill-filaments, 4 blunt, 4 longer and tapering; a pair of the latter type on the penultimate segment also (Figs 39.12A, B) ..... **Tanyderidae** (p. 742)
- Not with the above combination of characters ..... 14
- 14(13). Usually with a pair of partially or completely fused prolegs on thorax and a pair at apex of abdomen; body hairs, if present, normal; head without conspicuous internal pharyngeal skeleton (Figs 39.13G, H) ... **Chironomidae** (p. 744)
- Without prolegs or, if present, posterior pair completely fused; or head with conspicuous internal pharyngeal skeleton; or body hairs rising from sclerotised tubercles or plaques; sometimes extremely elongate (Figs 39.13B, C) ..... **Ceratopogonidae** (p. 746)
- 15(12). Integument finely pilose; thorax and abdomen with marked secondary segmentation; amphipneustic, posterior spiracles surrounded by 4 protuberances fringed with hairs, or set in a circular depression fringed with long hairs (Fig. 39.12D) ..... **Trichoceridae** (p. 742)
- Not with the above combination of characters ..... 16
- 16(15). Abdomen with the main portion of each segment separated from its neighbour by a narrow ring-like secondary segment; amphipneustic; body cylindrical, smooth, without conspicuous hairs or tubercles (Fig. 39.14B) ..... **Anisopodidae** (p. 747)
- Not with the above combination of characters ..... 17
- 17(16). Integument with conspicuous hairs or fleshy processes and usually dark, rather 'leathery'; metathoracic spiracle usually distinct (Fig. 39.14C) ..... **Bibionidae** (p. 748)
- Integument smooth, usually pale; no metathoracic spiracle ..... 18
- 18(17). Head black, shiny, centre of ventral surface with epicranial plates almost, but not quite, meeting at apices of a pair of short, blunt projections; abdomen without transverse rows of tiny spines ventrally (Fig. 39.14D) ..... **Sciaridae** (p. 749)
- Head otherwise, centre of ventral surface with epicranial plates broadly, or not at all, approximated, or joined by a complete narrow bridge; abdomen often with paired, transverse rows of tiny spines ventrally (Fig. 39.14E) ..... **Mycetophilidae** (p. 749)

### Division TIPULOMORPHA

Long-legged and long-winged flies, mostly with a generalised venation, including 2 distinct anal veins and Rs often 4-branched. They retain the primitive V-shaped suture and bilobed postphragma of the mesonotum, have distinguishable sex-chromosomes (except in limoniine Tipulidae), and form chiasmata at spermatogenesis. Larvae are mostly aquatic or semiaquatic, and meta-pneustic or amphipneustic.

**1. Tipulidae** (crane flies, daddy-long-legs; Figs 39.5A, B, 8A, 12C, 15). An immense family, cosmopolitan in distribution, with a world total of over 11 000 known species. In Australia, as elsewhere, it is by far the richest in species of all families of Diptera. Most Tipulidae are readily recognised by their slim build and long, unusually brittle legs, though the Trichoceridae and Tanyderidae have a very similar appearance. They are amongst the most generalised of Diptera, with a strong, V-shaped mesonotal suture and 2 complete anal veins, but lack ocelli and sometimes the discal cell. The interpretation of the venation (Figs 39.15D, F) is that proposed by C. P. Alexander (1929). In some of the larger species, the sexes differ strikingly in colour pattern, while the females of some species have vestigial wings. There is remarkable variation in size, from *Leptotarsus imperatorius* (Fig.

39.15F), one of our largest Diptera, with a wing-span of 75 mm, down to tiny, midge-like species of *Tasiocera*, expanding only 6–8 mm.

The family is well represented in Australia. Most species have been described from the mountainous areas of the south-east, and no doubt many more await recognition. They are notable lovers of moisture, usually found resting on foliage, overhanging banks, etc., in damp shady places. Some occur in very narrowly restricted habitats; e.g. at least one species appears to rest by preference on spider webs. Many of the smaller species are crepuscular, while a number of species, large and small, are attracted to light. The larvae (Fig. 39.12C) are hemicephalic, and found either in water or, more commonly, in wet soil or decomposing vegetable matter.

The following key will place most specimens in the subfamilies currently recognised (some authors regard them as separate families). It must be noted that there are exceptions to many of the individual characters given.

#### Key to the Subfamilies of Tipulidae

1. Last segment of palp almost always elongate, whiplash-like (Fig. 39.15A); antenna with not more than 15 segments (usually not more than 13); Sc usually ending in R; *m-cu* meeting  $M_{3+4}$  close to its



- fork or more distally on  $M_4$ ; mostly larger species ..... TIPULINAE
- Last segment of palp short, subequal to the others (Fig. 39.15B); antenna with less than 13 segments (*Hexatoma*) or with 14–39 segments; Sc ending in costa; *m-cu* usually joining M at, before, or only a short distance beyond its fork; mostly smaller species or of moderate size ..... 2
- 2(1). Wing with *r-m* joining Rs at or before the fork;  $R_{1+2+3}$  apparently with a long fusion back from the margin ..... CYLINDROTOMINAE
- Wing with *r-m* joining  $R_{4+5}$  or  $R_5$  beyond the fork of Rs (except in *Helius*); radial veins without such apparent fusion ..... LIMONIINAE

Australia is rich in endemic genera of TIPULINAE (8 out of 19), including the large, handsome and rather rare

species of *Clytocosmus* (Plate 5, K). Several genera occur also in New Zealand, South America and some in South Africa, whereas *Tipula* and *Nephrotoma* are world-wide genera which have invaded the continent only in the north. *Ptilogyna* and *Leptotarsus* include a number of species with subapterous females.

The CYLINDROTOMINAE are represented only by the endemic *Stibadocerodes*. The vast subfamily LIMONIINAE, however, is represented here by 5 tribes. Of these, the Lechriini have the single genus *Lechria*, which is entirely Austro-Malayan, while the more or less cosmopolitan Pediciini have only 2 species of *Pedicia* (*Tricyphona*) recorded from this country. In the Limoniini, the great genus *Limonia* has several characteristic subgenera, notably *Dicranomyia* and *Geranomyia*. *Idioglochina* has 2 northern species which, like those found in the Pacific

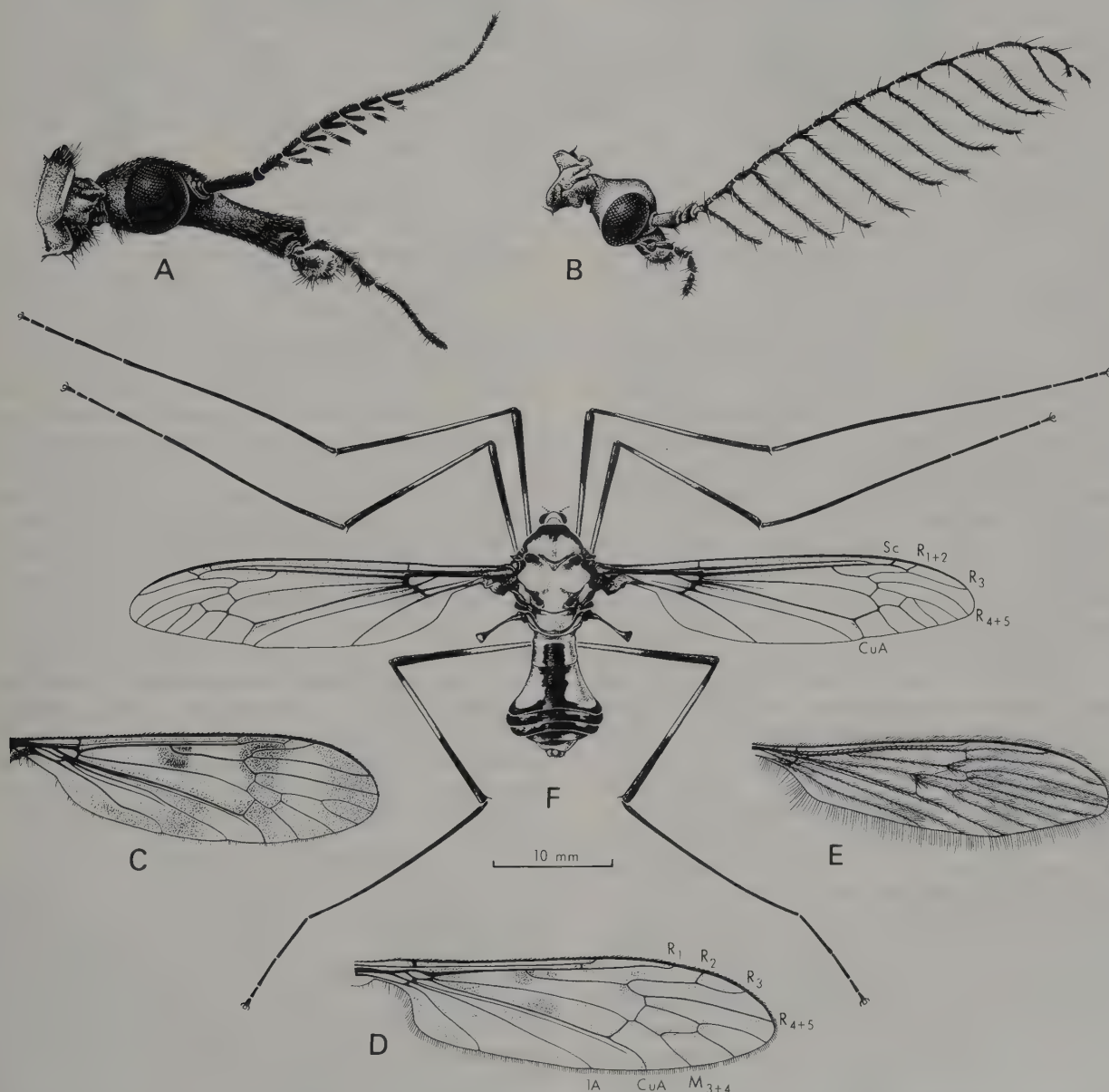


Fig. 39.15 Tipulidae: A, *Ptilogyna ramicornis*, ♂; B, *Paralimnophila setulicornis*, ♂; C, *Gynoplistia apicalis*; D, *Atarba australasiae*; E, *Molophilus* sp.; F, *Leptotarsus imperatorius*. [T. Binder]

islands, are probably marine. *Tonnoiromyia* is of particular zoogeographical interest, with 2 species in south-eastern Australia and one in Chile.

In the Hexatomini, which resemble some Trichoceridae in having small tibial spurs, there are 5 endemic genera and a number showing an 'Antarctic' distribution: of the latter, *Gynoplistia* (Fig. 39.15C) and *Atarba* (Fig. 39.15D) are most characteristic. Of the cosmopolitan genera, there are *Limnophila*, with many Australian species, and the aptly named *Elephantomyia*, which has a long, superficially mosquito-like proboscis. Both *Limnophila* and *Gynoplistia* include species with subapterous females, and, in the latter, subapterous males also.

The Eriopterini are mostly small flies, many of which lack a discal cell in the wing. They are most abundantly represented in Australia by the genus *Molophilus* (Fig. 39.15E), with about 150 species, some with subapterous females. The genus is also well developed in New Zealand and Chile. *Tasiocera* is another characteristic Australian genus with a somewhat similar 'Antarctic' distribution. [C. P. Alexander 1932, and numerous short papers, from 1923 onwards; Dobroworsky 1974]

**2. Trichoceridae** (Petauristidae; winter crane flies; Fig. 39.7B). A small, primitive family, including only 4 genera. Superficially, they resemble the Tipulidae, but they have ocelli and a eucephalic larva. The morphology of the immature stages has led some authors to ally them with the Anisopodidae. All are small, delicate, long-legged, brownish flies, with a wing-span of about 10–12 mm, and, like the Tipulidae, are found in damp, shady places. They are so far known only from the cooler areas of south-eastern Australia, and are commonly found only in the colder months of the year. Most appear to be crepuscular or nocturnal in habit, and they are often taken in light traps. The larvae occur principally in decomposing vegetable matter, and several species have been reared from rotting mushrooms.

*Trichocera*, a Holarctic genus with small tibial spurs, is represented by the introduced European *T. annulata*. *Paracladura*, found in various countries around the Pacific, has a single undescribed Australian species, recognisable by the extremely short basitarsus. There are also 4 species of *Nothotrichocera* (Fig. 39.7B), with normal tarsi and no tibial spurs; the genus is known elsewhere only from the subantarctic Campbell and Auckland Is. [C. P. Alexander 1926]

### Division TANYDEROMORPHA

Moderate to large flies, with long legs, no ocelli, and patterned wings; Rs and M both 4-branched and discal cell present. The pronotum and neck sclerites are strongly developed, giving a 'long-necked' appearance. Superficially they resemble Tipulidae, but have the V-shaped suture of the mesonotum incomplete, postphragma almost completely fused, vein 2A reduced to a relic at the wing base, and the mouth-parts elongate, with functional mandibles.

**3. Tanyderidae** (Figs 39.12A, B, 16A). An essentially Australasian family, and amongst the most primitive in the Diptera. Adults are usually found together with

Tipulidae in moist forest habitats. The only known Australian larva (*Eutanyderus* sp.) is eucephalic and apneustic, with a series of long gill-filaments at the apex of the abdomen; two filaments arise from small prolegs (Fig. 39.12B). The Australian larva bores in the surface layers of submerged rotting logs in alpine streams. All Australian species are rare, some known from single specimens only. There are 2 endemic genera, *Nothoderus* (1 sp.) and *Eutanyderus* (2 spp.), the latter closely related to a South American genus. The other 3 species fall in *Radinoderus*, an essentially tropical genus; *R. occidentalis* is particularly interesting in being recorded only from south-western W.A. [C. P. Alexander 1938; Colless 1962b; Hinton 1966a]

### Division BLEPHARICEROMORPHA

Adults long legged, not unlike Tipulidae, and some with complete V-shaped mesonotal suture; but wings with characteristic network of pseudovenation (Figs 39.18B, C), produced by folding within the pupal wing-cases. In life, wings held out at right angles to body. Mouth-parts elongate, female (but not male) with long, spear-like mandibles. Malpighian tubules extremely distinctive, asymmetrically distributed, 2 on left side, 3 on right (Zwick 1977b). Immature stages aquatic, attaching to stones by means of suckers (larvae) or adhesive pads (pupae). Relationships to other groups are obscure. They share the fused postphragma and certain cytogenetic features with Bibionomorpha, but there are other points of resemblance to Culicomorpha and Tanyderomorpha.

**4. Blephariceridae** (Figs 39.3A, 14A, 18B, C). An archaic, cosmopolitan family of unusual interest, both zoogeographically and in the bizarre immature stages. *Edwardsina* alone retains the V-shaped mesonotal suture and fairly complete venation. Adults are found in the vicinity of fast-flowing streams and waterfalls; some species tend to congregate on rocks close to the water, but others are most elusive and rarely seen. The aquatic immature stages attach to stones in fast-flowing water, often in the splash-zone of cascades.

The Australian fauna has 18 species of *Edwardsina* in the highlands of south-eastern Australia and Tas., plus some 7 species in 3 genera of Apistomyiini (*Apistomyia*, *Parapistomyia* and *Austrocurupira*), which extend into the tropics. *Edwardsina* has its closest relatives in Madagascar and Chile, while the apistomyiine genera have theirs in Asia and Europe; the zoogeographic implications are still unclear. [Zwick 1977b, 1981b]

### Division CULICOMORPHA

Mostly small, delicate flies (except for the more stoutly built Simuliidae and Thaumaleidae), lacking the V-shaped mesonotal suture, and with rather specialised venation. Almost all have 3 or 4 pairs of chromosomes, and the X and Y chromosomes are poorly, if at all, distinguishable. Several families show a high frequency of sibling species complexes, their members distinguishable only or mainly by chromosomal structure.

**5. Chaoboridae.** A small cosmopolitan family, represented in Australia by 4 genera, 2 of them (*Promochlonyx*





Fig. 39.16 A, *Eutanyderus oreonympha*, Tanyderidae, ♂; B, *Atrichobrunnattia alternata*, Psychodidae, ♀.

[T. Binder]

and *Australomochlonyx*) endemic. Adults resemble mosquitoes, but lack the long biting proboscis; nonetheless, *Corethrella* is known to suck blood. Larvae are aquatic. They have a respiratory siphon on abdominal segment 8 or (*Chaoborus*) are apneustic, respiring through the integument. All but *Corethrella* control their buoyancy by means of pigmented tracheal air-sacs (which are practically all that can be seen of the otherwise transparent larvae of *Chaoborus*). Only *Chaoborus* species are common; their adults can be a minor pest around lights and larvae sometimes block filtration plants in water supplies. Larvae of *Chaoborus*, *Promochlonyx* and *Corethrella* are predacious on other aquatic life, but those of *Australomochlonyx* are filter-feeders, straining micro-organisms from the water by means of their enormous mandibular fans. [Colless 1986]

**6. Dixidae** (Figs 39.12E, 17H). A small, cosmopolitan family, with 3 genera, only one of which occurs in Australia. All are small, with wing length about 3–4 mm, shiny integument, and characteristic venation. The adults rest on rocks or vegetation close to streams, generally under forest cover. The larvae are aquatic, usually in the meniscus on vegetation at the edge of flowing water, but may sometimes be seen swimming in the surface film with a characteristic jerky motion. Only the posterior spiracles are functional, with a complex apparatus of valves that allows them to be closed off. The Australian species, so far known only from the south-east, all belong to the

large genus *Dixa*. There are 6 or 7 species of the sub-genus *Nothodixa*, which also occurs in New Zealand and Patagonia. These have *r-m* placed well before the fork of Rs. The other species belong to the cosmopolitan *Paradixa*, with longer antennae and *r-m* at or after the fork. [Tonnoir 1923]

**7. Culicidae** (mosquitoes; Figs 39.2A, B, 12G, H, 17C, D). A large cosmopolitan family, with characteristic venation and with scales (sometimes very narrow) along the veins and posterior margin of the wing. Most species have elongate mouth-parts, forming the typical 'proboscis' of the true mosquitoes; its visible portion is formed by the fleshy labium wrapped around the fine stylets which, in blood-sucking species, are used to pierce the host's skin (Fig. 39.4). Males are more slender than females and, with rare exceptions, have strongly plumose, bushy antennae. Males are not blood-suckers, but females usually require a blood meal before their eggs can mature. There is considerable host specificity, and not all will normally attack humans. Many take blood from other animals, and some feed mainly on birds, reptiles or frogs; even fish ('mud-skippers', *Periophthalmus* sp.) are attacked. Mating usually takes place on the wing, and eggs are laid on free water or wet surfaces, both activities often involving highly specialised behaviour. Adults normally rest by day in shady, humid sites, flight activity commencing at sundown, but some species are active by day in shady places.

The larvae are all aquatic, taking in atmospheric oxygen at the surface by means of spiracles, borne dorsally on abdominal segment 8; these may be sessile (*Anopheles*) or at the apex of the sclerotised tube, the 'siphon' (Fig. 39.12H). One genus (*Mansonia*) takes air from the tissues of aquatic plants through a specially adapted, piercing siphon. Both larvae and pupae are very active swimmers, and dive rapidly when disturbed. All species show at least some restriction to a 'preferred' larval habitat, chosen by the ovipositing females: in permanent ground pools and streams, usually amongst emergent vegetation; in transient pools; or in a variety of container-habitats, some highly specialised (e.g. tree-holes, plant axils). All groups may include saline habitats; e.g. *Aedes australis* breeds in concentrated sea-water in seaside rock-pools. Some species (e.g. *Aedes aegypti*) are domestic, breeding mainly in containers around human dwellings.

Certain species are important vectors of disease (p. 229). In Australia malaria has been transmitted mainly by one or more members of the *Anopheles farauti* species-complex; filariasis by *Culex fatigans*; dengue fever by *Aedes aegypti*; and other arboviruses by several species, of which *Culex annulirostris* appears to be the most important (Lee *et al.* 1980–89; Russell 1987). Several also transmit myxomatosis of rabbits, and so perform a valuable economic function (Fenner and Ratcliffe 1965). Apart from disease transmission, mosquitoes can be a serious pest, disturbing the comfort of humans and affecting the productivity of domestic animals. Some major pest species are *Culex fatigans* (domestic), *C. annulirostris* (widespread), *Aedes vigilax* (coastal, breeding in brackish swamps) and *A. notoscriptus* (a widespread container-breeder); other species may be very abundant in particular localities.

#### Key to the Subfamilies of Culicidae

1. Abdomen with few or no scales, at least on the sternites; ♂ palps clubbed apically, ♀ palps usually about as long as proboscis; larval spiracles sessile ..... ANOPHELINAE
  - Abdomen completely clothed with scales; ♂ palps not clubbed, ♀ palps much shorter than proboscis; larva with siphon ..... 2
- 2(1). Proboscis with apical half ventrally recurved; scutellum evenly rounded; large, metallic species; larval mouth-brushes prehensile, each composed of 10 stout rods ..... TOXORHYNCHITINAE
  - Proboscis more or less straight; scutellum with 3 lobes; larval mouth-brushes rarely prehensile, with 30 or more hairs ..... CULICINAE

The ANOPHELINAE have only 2 Australian genera. The tropical *Bironella* is rare, but *Anopheles* has about 15 species, mostly tropical. Members of the *Anopheles annulipes* species-complex, with spotted wings (Fig. 39.17D), occur throughout the continent. Anopheline larvae are readily recognised in the field by their habit of lying suspended horizontally from the surface film; the adults' resting and feeding attitude is also characteristic, with proboscis and body in a straight line at an angle

to the surface. The TOXORHYNCHITINAE include only 3 Australian species of *Toxorhynchites*. The adults are large, handsome, with metallic coloration, and do not suck blood; the larvae are predacious, mainly on other mosquito larvae. The CULICINAE comprise the bulk of our mosquito fauna, with *Culex* and *Aedes* as the dominant genera; *Aedes* is represented by 11 subgenera, dominated by *Ochlerotatus* and *Finlaya*. There are 9 other genera, including the curious plant-axil-breeding *Malaya*, whose adults are fed by ants.

The bulk of the Australian fauna is derived from the tropics to the north. Many New Guinea species extend into the Cape York area, while *Mansonia uniformis* and *Aedes lineatopennis* range as far west as Africa. The domestic species, *C. fatigans* and *A. aegypti*, also are widely distributed in other regions. No genus is endemic, but there are several endemic subgenera, e.g. *Aedes* (*Chaetocruimyia*), and a number of characteristically Australian species-groups, particularly in the south. *Culiseta*, with 12 species and 2 endemic subgenera, is of particular interest, since, apart from one species in Africa and one in New Zealand, the genus is otherwise almost completely Holarctic. [Clements 1963; Dobrotworsky 1965; Fenner and Ratcliffe 1965; Lee *et al.* 1980–89]

**8. Chironomidae** (Tendipedidae; midges; Figs 39.2c, 13G, H, 17A, B). A large, cosmopolitan family, diverse in form but mostly small, delicate flies, some superficially resembling mosquitoes. They range in size from *Chironomus australis* with wing length 7.5 mm, down to the minute *Orthosmittia reyei* with wing length of only 0.8 mm. Many are brownish or black, but green, reddish and yellow species occur, and the wings are sometimes hairy, and sometimes with dark markings. In almost all species, the male antennae are strongly plumose (Fig. 39.17A), and some show sexual dimorphism in colour pattern. The primitive relict *Archaeochlus* is unique in possessing mandibulate, biting mouth-parts, very like those of some Ceratopogonidae.

Adults are common, particularly in the vicinity of bodies of water. They are mainly crepuscular or nocturnal, often forming mating swarms at sundown, and can occur in such enormous numbers as to cause considerable annoyance around lights on warm evenings. Several species (*Clunio*, *Telmatogeton*) are marine, the adults occurring on intertidal rocks; in *Clunio*, the female is wingless. Also, the extraordinary marine genus *Pontomyia* (Fig. 3.9) has an apterous, vermiform female and the male wings are reduced to paddle-like structures. In a number of genera, adults are frequently parasitised by mermithid worms, usually resulting in partial feminisation of males.

The larvae are, with few exceptions, aquatic, living either buried in the bottom debris or free on vegetation; many of the former live enclosed in a gelatinous tube coated with particles of debris. One species damages rice seedlings in N.S.W., principally through physical disturbance of the roots. The tube-dwellers include the 'blood-worms', whose colour is due to haemoglobins in the haemolymph. These pigments have been implicated in widespread allergic reactions of humans to midge larvae



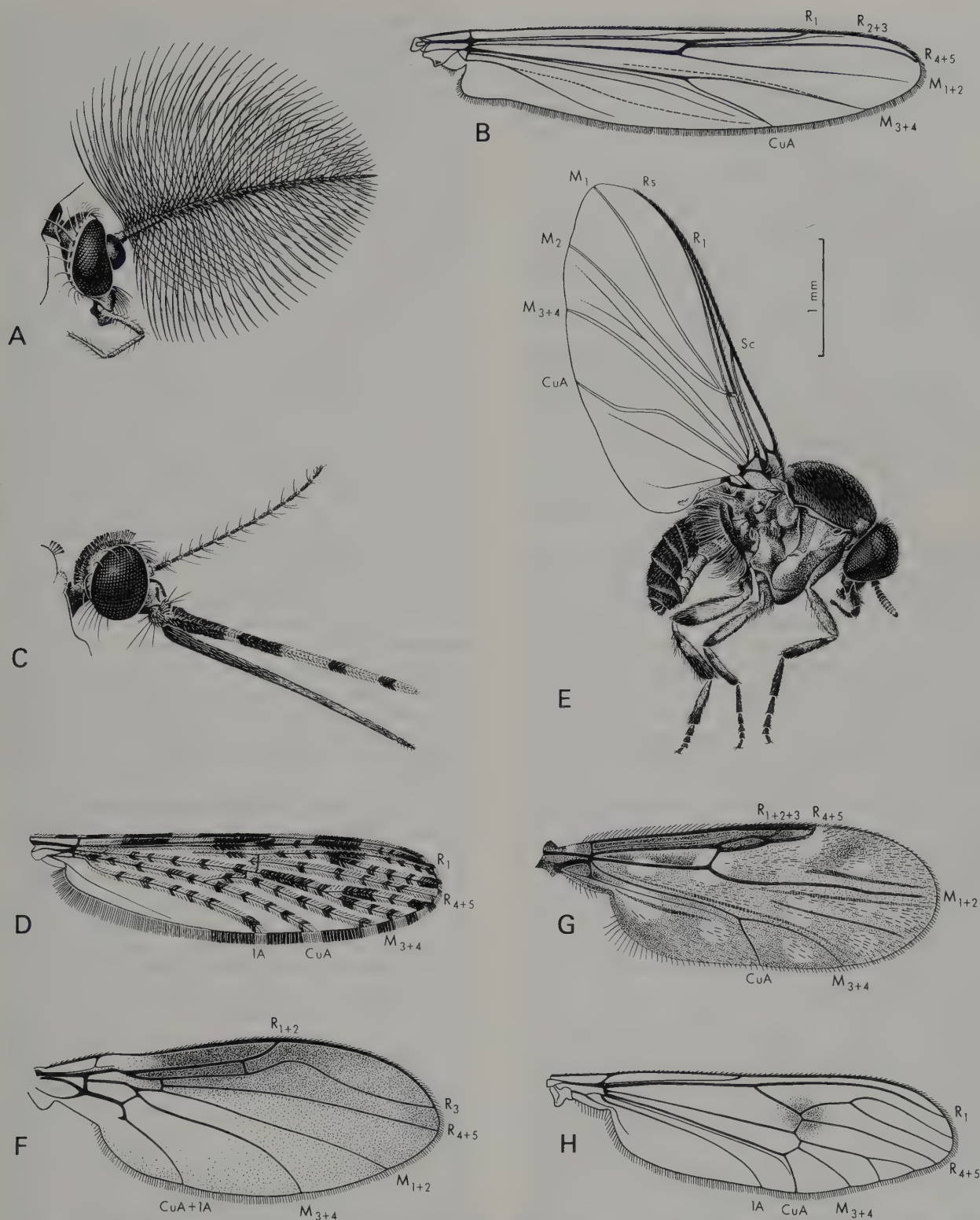


Fig. 39.17 Culicomorpha: A, *Chironomus alternans*, Chironomidae, ♂, head, lateral; B, same, wing; C, *Anopheles annulipes*, Culicidae, ♀, head, lateral; D, same, wing; E, *Simulium ornatipes*, Simuliidae, ♂; F, *Austrothaumalea* sp., Thaumaleidae; G, *Culicoides antennalis*, Ceratopogonidae; H, *Dixia nicholsoni*, Dixidae. [T. Binder]

and adults (Cranston *et al.* 1983). In *Paraborniola* and *Allotrissocladius*, larvae are highly drought adapted, surviving in a partly hydrated state in dried-out pools.

Typically, the larvae bear a pair of prolegs on the prothoracic and anal segments, and a pair of papillae, each with a tuft of hairs, on the anal segment.

*Key to the Subfamilies of Chironomidae*

1. Base of  $M_{3+4}$  (*m-cu* of authors) present ..... 2  
    Base of  $M_{3+4}$  absent (Fig. 39.17B) ..... 4
- 2(1).  $R_1$  and  $R_{4+5}$  widely separated,  $R_{2+3}$  absent. (Postnotum without median furrow) ..... PODONOMINAE  
     $R_{2+3}$  usually present; if absent,  $R_1$  and  $R_{4+5}$  separated by no more than width of a vein ..... 3
- 3(2).  $R_{2+3}$  usually forked; if simple or absent, then wing with dense macrotrichia ..... TANYPODINAE  
     $R_{2+3}$  simple; wing bare ..... DIAMESINAE
- 4(1).  $R_{2+3}$  absent;  $R_1$  and  $R_{4+5}$  widely separated ..... 5  
     $R_{2+3}$  usually present; if absent, then  $R_1$  and  $R_{4+5}$  very close ..... 6
- 5(4). Fourth tarsal segment cordiform; male genitalia enlarged and (variably) rotated ..... TELMATOGETONINAE  
    Fourth tarsal segment cylindrical; male genitalia small, not rotated ..... APHROTENIINAE
- 6(4). Fore leg with basitarsus shorter than tibia; male styles flexibly attached to coxites ..... ORTHOCLADIINAE  
    Fore leg with basitarsus subequal to or (usually) longer than tibia; male styles rigidly attached to coxites and directed backwards ..... CHIRONOMINAE

Eighty-six genera are so far known from Australia, with the Podonominae, Orthocladiinae and Tanypodinae more numerous in the colder areas of the south-east, and the Chironominae more abundant in the hotter regions. No doubt many species await recognition, since some are now known that are distinguished mainly by cytological features (e.g. Martin 1963). Three elements can be recognised in the fauna. (a) Typical members of well-known cosmopolitan genera (e.g. *Chironomus*, *Polypedium*, *Tanytarsus*); the majority of species fall in this group, including 8 which are apparently identical with forms known from other regions (e.g. the Palaearctic and Oriental *Polypedium nubifer*). (b) A small group of probably primitive genera, which have an 'Antarctic' distribution (e.g. *Austrocladius*, common during the winter, and also found in New Zealand, Patagonia and southern Chile); also *Archaeochlus*, known only from W.A. and South Africa. (c) Twelve endemic genera, which include some 22 species. [Edward 1986; Cranston *et al.* 1987; Pinder 1986 (biology)]

**9. Ceratopogonidae** (Heleidae; sand flies, biting midges; Figs 39.13B, C, 17G). A widespread family of small to minute blood-sucking flies, not to be confused with the phlebotomine 'sand flies' (Psychodidae). A few genera, e.g. *Johannsenomyia*, have species with wing spans up to 5 mm, but most are much smaller. All have somewhat elongate, piercing mouth-parts, usually associated with a predatory or blood-sucking habit, and many are notable pests of vertebrates. Other animals also are attacked, including insects; e.g. *Pterobosca* spp. are found on the wings of dragonflies, while *Culicoides anophelis* is a secondary blood-sucker, feeding on blood from the abdomens of engorged mosquitoes. Those most commonly encountered in Australia are the pest species of *Culicoides* and *Leptoconops*, whose attacks cause severe annoyance and, particularly in the tidal zone, may render areas barely fit for human habitation. Some species are

proved vectors of viruses and parasitic worms in other countries; e.g. blue-tongue of sheep, *Onchocerca* spp. of cattle and horses, and several minor filariases of humans. In Australia *Culicoides brevitarsis* has been incriminated as causing an allergic dermatitis of horses and (probably) a virus disease of cattle (Akabane disease). Other arboviruses have been isolated from *Culicoides* species, and some species are potential vectors of blue-tongue disease of sheep, should it ever enter Australia (Debenham 1978). Not all ceratopogonids are predatory; some frequent flowers, and the cocoa plant depends upon species of *Forcipomyia* for pollination. Apart from those taken biting, adults sometimes enter light traps in large numbers, and many can be swept from vegetation. The tiny larvae are more elusive, living mainly in mud or debris in or around ground-water or container habitats, or in rotting vegetation; some occur in tree-holes and rock-pools. A number of species, including some notable pests, breed in saline or brackish habitats.

The general composition of the Australian fauna is now fairly clear. The dominant genus is *Culicoides* (Fig. 39.17G), while 27 others are known to occur here, the richest in species being *Dasyhelea*, *Forcipomyia* and *Atrichopogon*. The ease of dispersal of these small flies is reflected in the fact that at least 15 of our genera, including the 4 above, have world-wide distributions. However, *Austroconops* is apparently endemic; *Macrurohelea*, *Acanthohelea* and *Paradasyhelea* also occur in the Neotropical region; while *Xenohelea* and *Dibezzia* (Oriental and Ethiopian regions) are examples of a northern element. [Debenham 1978, 1987; Reye 1971; Hagan and Reye 1986; Borkent *et al.* 1987]

**10. Simuliidae** (Melusinidae; black flies; Figs 39.2E, 13F, 17E). A cosmopolitan family of biting flies, readily recognised by their stout build and wings with large anal lobe and characteristic venation. All are relatively small, with wing length 1.5–3.5 mm, and most are dark in colour. Some species require a blood meal for maturation of the eggs, and *Austrosimulium pestilens* is a vicious pest of humans and animals in Qld. Its eggs can lie dormant in damp river sediments for long periods, to hatch after floods (Colbo and Moorhouse 1974). *A. bancrofti* is another widespread feeder on stock, and other species are troublesome in Tas. and southern Australia. In general, however, adults are infrequently encountered, usually swept from vegetation near streams or taken in light traps. Larvae and pupae are more readily found, attached to stationary objects in running water. There are specific differences in rates of flow tolerated and types of substratum preferred. The larva and pharate pupa (Hinton 1958a) move about with a caterpillar-like motion and breathe by means of anal gills, whereas the pupa and pharate adult have thoracic gill-tufts. Pupae are enclosed in small silken cocoons.

The 3 genera found here present in miniature much of the zoogeographical picture of the Australian fauna as a whole. Species currently placed in *Cnephia* and possibly some *Austrosimulium* show the 'Antarctic' pattern; the first group may have related species in South America, and the latter has congeneric relations in New Zealand



(Dumbleton 1963). However, *Simulium* appears to be derived from the north; one group of species occurs only in the northern half of the continent and in New Guinea, with related species in Indonesia, while the *S. ornatipes* complex (Fig. 39.17E) occurs throughout Australia and extends into New Guinea and New Caledonia. [Colbo 1976; Bedo 1979]

**11. Thaumaleidae** (Orphnephilidae; Figs 39.13D, E, 17F). A small family of stoutly built flies, the Australian species with a wing-span of only 5–10 mm. The venation is very characteristic, and the wings also have a peculiar tendency to fold downwards, across a transverse line of weakness near the apex of Sc. The systematic position of the family is puzzling. Most authorities place them near the Chironomidae, but cytogenetically they seem closer to the Bibionomorpha. Little is known of their biology. Adults are occasionally swept from wet rocks or vegetation near streams in wet forest, and the larvae are aquatic, superficially resembling Chironomidae. The family is of considerable zoogeographic interest. All Australian species belong in *Austrothaumalea* (18 species) or *Niphta* (3 species), both of which have other members in New Zealand and/or South America (Theischinger 1986).

### Division PSYCHODOMORPHA

Small to large flies with generalised wing venation; Rs and M both 4-branched (except in *Trichomyia* and *Sycorax*, with Rs 3-branched). Mesonotum without complete, V-shaped suture; postphragma partly fused, but with distinguishable lobes; metathorax usually better developed than in other Diptera. As far as known, cytogenetic details resemble those of the Culicomorpha. Although poorly represented as fossils, they appear to represent a distinct and probably very ancient lineage.

**12. Psychodidae** (moth flies; Figs 39.12F, 16B). A cosmopolitan family of small flies, with wing-span rarely exceeding 8 mm, usually much less. In most, the wings are broadly ovate, pointed, hairy and folded roofwise over the abdomen; this and the hairy body together give them a moth-like appearance. In all but a few genera, both Rs and M are 4-branched and the anal veins greatly reduced.

Adults frequent moist, shady places, but are rarely seen on the wing; at least some are nocturnal and come to light. They are most abundant in early summer, but *Psychoda* is also common during the winter. Most are short lived (1–2 days) and do not feed, except for members of the blood-sucking Phlebotominae. In certain countries, where they are often called 'sand flies', species of *Phlebotomus* are important vectors of kala-azar, other forms of leishmaniasis, and the viruses of 'sand fly fever'. Although inconspicuous, *Phlebotomus* are relatively common in Australia and are known to harbour arboviruses (Doherty *et al.* 1973). Psychodid larvae feed on decomposing organic matter, usually at the edges of freshwater habitats or in rotting vegetation and dung, although *Trichomyia* probably bores in wood. *Pericoma* and *Telmatoscopus* have a long larval life and require permanent moisture, but the shorter-lived *Psychoda* can exploit more temporary habitats. *Psychoda alternata* is sometimes a pest of sewage-treatment plants and is often

seen in bathrooms. The Australian fauna is not yet well known, but most genera occur here, including such rarities as *Nemopalpus*, *Sycorax* and *Trichomyia*. Those commonly encountered are *Psychoda*, *Pericoma*, *Brunettia* and *Telmatoscopus*. [Duckhouse 1965; Lewis and Dyce 1988]

### Division BIBIONOMORPHA

Mostly rather stoutly built flies, but some very small; characterised by the more or less complete fusion of the lobes of the postphragma, which is often strongly developed and may project well into the base of the abdomen; also by the absence of chiasma formation during spermatogenesis. The venation tends to be reduced, with Rs at most 3-branched and the basal portion of M often missing. Larvae are terrestrial. Those of Anisopodidae, Scatopsidae and, to some extent, Perissommatidae show many resemblances to Psychodidae, and may be poorly placed in Bibionomorpha. Certain family groupings can be discerned, e.g. Mycetophilidae-Sciaridae-Cecidomyiidae, but no useful scheme of superfamilies is yet apparent.

**13. Anisopodidae** (Rhyphidae, Phryneidae, Sylvicolidae; Figs 39.2D, 3B, 10A, 14B, 18A). A rather small family, often postulated as most closely resembling the ancestors of the Brachycera. All are stoutly built flies of moderate size, and the common genus *Sylvicola* has attractively mottled wings. *S. dubius* is very common in temperate Australia during the cooler months, usually in moist forest, but it also occurs in semi-domestic situations. All species breed in decomposing organic matter, *Olbiogaster* being apparently restricted to rotting wood. *Sylvicola* larvae, which frequent more liquid media, are extremely active; their posterior spiracles can be retracted and sealed off during submergence. The family is poorly represented here, with only 3 species of *Sylvicola* and one (rare and undescribed) of *Olbiogaster*. The latter genus falls in a small group of presumably archaic Nematocera, that have curiously disjunct, pantropical distributions (Stuckenberg 1962). [Fuller 1935; G.H. Hardy 1967]

**14. Perissommatidae** (Figs 39.14F, 18D, E). A very small family including only the 5 known species of *Perissomma*. All are small flies with a characteristic venation and 3 species have mottled wings. The eyes are remarkable in being divided into separated dorsal and ventral components. Adults have been found during the winter months only and are rarely encountered, except for *P. fusca*, which breeds in large numbers in decomposing fungi in plantations of introduced pines. Also, females of *P. bellissima* have been taken in fair numbers at micro-carrion. The larva pupates within the unmodified larval skin and is well adapted both to life in a semi-liquid medium and to aestivation during summer drought. It resembles Anisopodidae in having a complete, transverse (posterior) tentorium (the larva tentatively ascribed to *Perissomma* by Colless, 1969c, is now thought to be a coleopteran). The genus is 'Antarctic', occurring in sclerophyll and rain forests in south-eastern Australia and southern South America. [Colless 1969c; Duret 1976]

**15. Scatopsidae** (Figs 39.14G, 19B). Small to minute

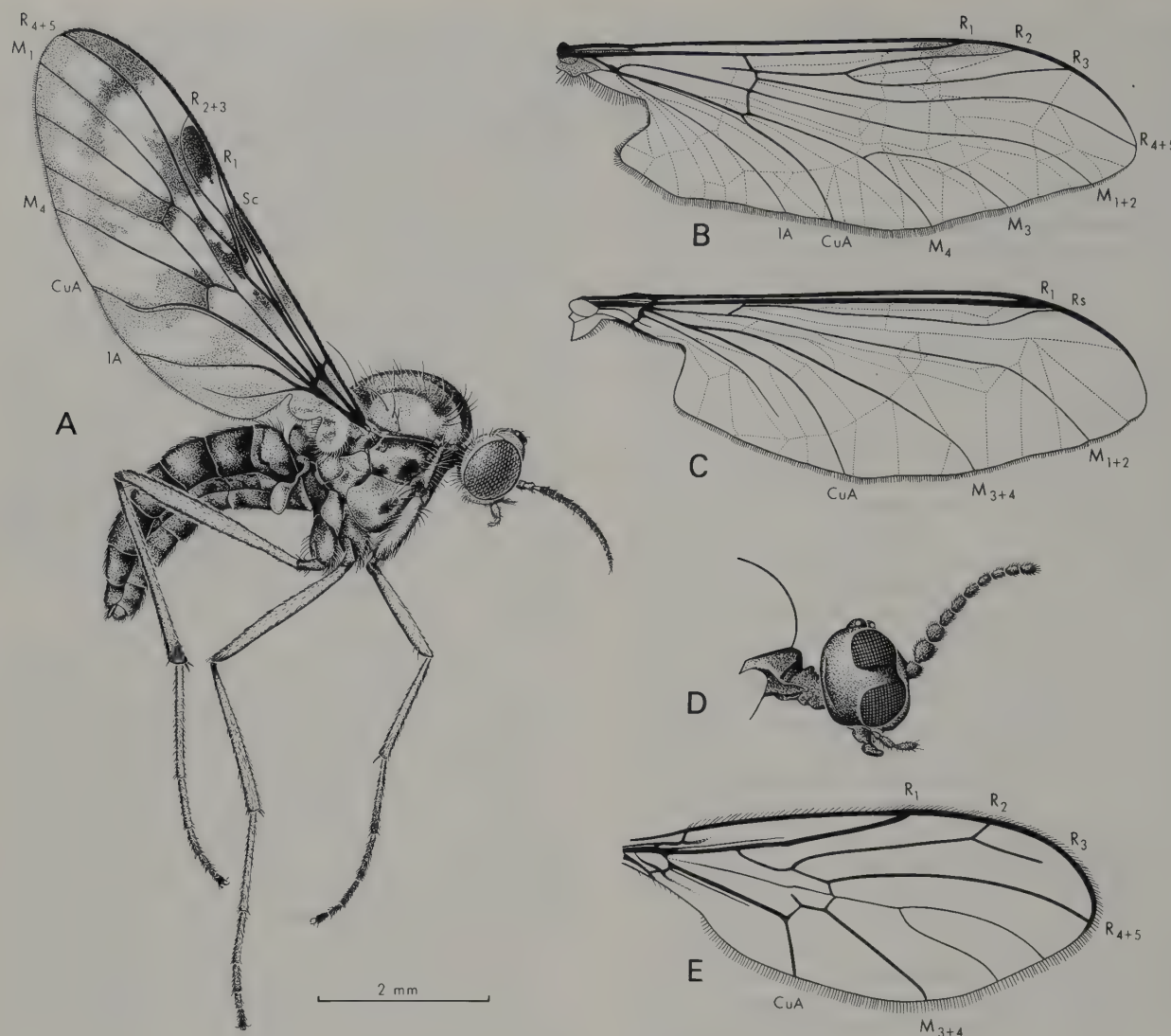


Fig. 39.18 A, *Sylvicola dubius*, Anisopodidae; B, *Edwardsina* sp., Blephariceridae; C, *Apistomyia tonnoiri*, Blephariceridae; D, *Perissomma fusca*, Perissommatidae, head, lateral; E, same, wing.

[T. Binder]

flies, predominantly black in colour, with 1-segmented palps and the radial veins thickened and dark. They are not commonly encountered or collected, except for the introduced *Scatopse notata* and *S. fuscipes* which thrive in peridomestic habitats. At least some Australian species are confined to wet forest. Larvae occur in rotting vegetable matter and dung, and the pupae are enclosed in the last larval skin, with only their branched respiratory horns protruding. The Australian fauna is relatively rich, with over 50 species in 12 genera, more than half in *Colbostema* and *Rhegmoclema*. *Hawomersleya* and *Austroclemina* are endemic, and the rest mainly cosmopolitan. [Cook 1971, 1977]

**16. Bibionidae** (Figs 39.14C, 19A). Flies of small to moderate size, some species of *Plecia* expanding 20–25 mm. The structure of the head is particularly characteristic, and males are all holoptic, almost always with each eye differentiated into a large anterodorsal section and small posteroventral section. Adults are rather sluggish

and poor fliers, and most species inhabit forest. Some are active by day, but flight activity is probably mainly crepuscular and nocturnal; they are common in light traps. The larvae occur in decomposing vegetation and in the soil; some feed on plant roots, but probably on dead tissue. In Australia, *Bibio imitator* sometimes occurs in very large numbers in garden soil, but does not attack living plants.

The tropical genus *Plecia* (Plate 6, ZA), with smoky wings, usually orange thorax, and  $R_s$  branched, is dominant in the north, though the small *P. dimidiata* is mainly southern. *Dilophus* (Fig. 39.19A), which has 2 transverse rows of blunt teeth on the thorax, is dominant in southern areas (as also in New Zealand and southern South America). *Bibio*, with fore tibia produced into a large apical spine, is represented mainly by *B. imitator*, which, like many *Dilophus*, has pale brown females and dark males. A second species of *Bibio* is shared with New Guinea, as is the curious *Enicoscolus collessi*, with short-



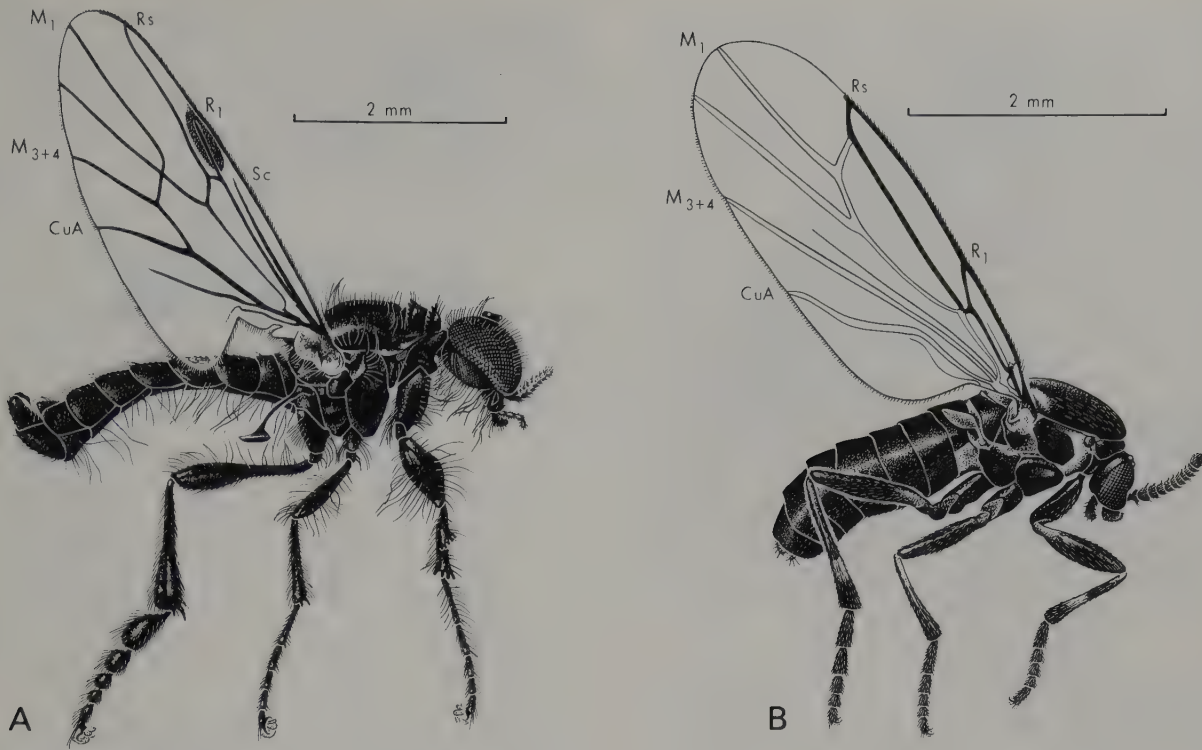


Fig. 39.19 Bibionomorpha: A, *Dilophus* sp., Bibionidae; B, *Scatopse notata*, Scatopsidae.

[T. Binder]

ened costa and  $M_{3+4}$  not connected with  $M_{1+2}$ . The genus is otherwise known only from Mexico. [D. E. Hardy 1982]

**17. Cecidomyiidae** (Itonididae; gall midges; Figs 39.14H, 20E). A large, cosmopolitan family of small to minute flies, most with delicate hairy wings and reduced venation (*Lestremia* resembles the Sciaridae in venation, but has no tibial spurs). The adults are ubiquitous, and their small size and active flight habits make them very susceptible to dissemination by air currents. Many show a remarkable tendency to congregate unharmed on spider webs. Many larvae, when mature, have a characteristic, longitudinal, sclerotised 'sternal spatula' on the prothoracic sternum. Most live in galls or other deformities in living plants; and at least some feed there on fungi that are introduced by the ovipositing female (Borkent and Bissett 1985). Others are scavengers in decomposing organic matter and some are paedogenetic. Various exotic species are predacious on aphids and other small arthropods, while a few are endoparasites, or live as inquilines in insect galls. No doubt species with similar habits occur here also. In other countries, the plant parasites include some very destructive crop pests, e.g. *Mayetiola destructor*, the Hessian fly of wheat; but, as far as is known, the sorghum midge, *Contarinia sorghicola*, is the only serious pest so far established in Australia. *Zeuxidiplosis giardi* is a beneficial species introduced for the control of St John's wort, while species of *Arthrocnodax* and *Lestodiplosis* prey upon orchard mites. Almost all Australian known species were described by Skuse (1888a, 1890), who gives an interesting account of their

biology; they have been little studied since then. Most of the well-known genera occur in Australia, and we think probably there are a number of immigrant species. The aberrant *Ipomyia* is apparently endemic (Colless 1965).

**18. Sciaridae** (Lycoriidae; Figs 39.8B, 14D, 20C, D). An extremely widespread family, with members adapted to a wide variety of climates. Their uniformity of structure makes taxonomic treatment very difficult, and our fauna badly needs revising, using modern generic concepts (Tuomikoski 1960). Sometimes treated as a subfamily of Mycetophilidae, they resemble that family in adult habits, but at least some are much more active by day in more open situations. They are, however, common in light traps, some of the rainforest species being taken in very large numbers. One apterous species of *Austrosciara* is an inquiline in termite nests. Sciarid larvae, usually with pale body and shiny black head-capsule, tend to be gregarious, and are commonly found in rotting vegetable matter or highly organic soils; a species of *Bradysia* attacks roots of plants in greenhouses, and *Lycoriella agarici* is a major pest of cultivated mushrooms. The Australian fauna probably includes most of the described genera and possibly some immigrant species. The aberrant genera *Colonomyia* and *Ohakunea* are currently lodged in this family, on somewhat dubious grounds. The former is otherwise known only from the mountains of New Guinea, but the latter has one closely related species in southern Chile and another, less closely related, in New Zealand. [Skuse 1888b; Colless 1962a; Steffan 1966; Loudon 1978]

**19. Mycetophilidae** (Fungivoridae; fungus gnats; Figs

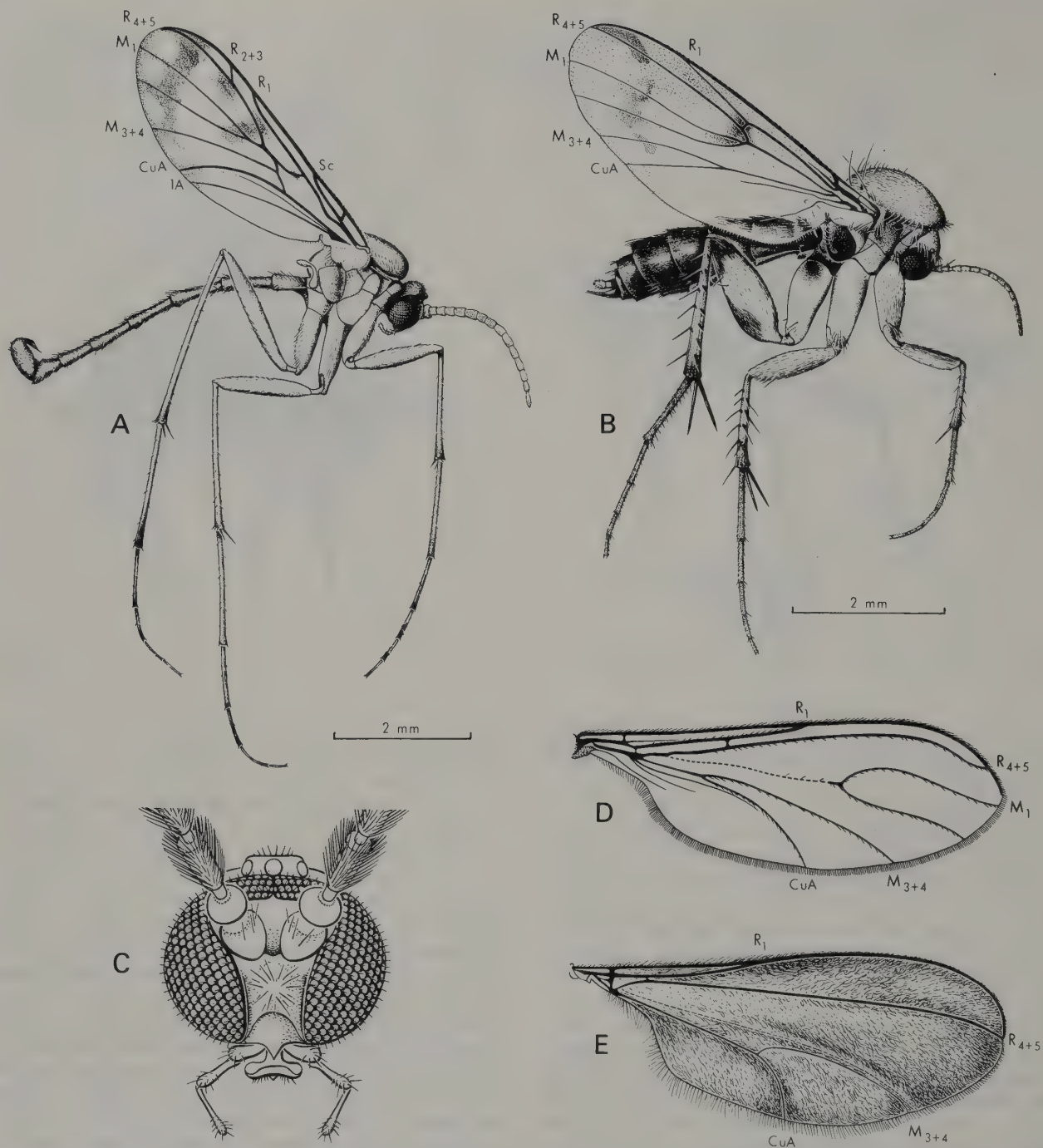


Fig. 39.20 A, *Orfelia fenestralis*, Mycetophilidae, ♂; B, *Mycetophila propria*, Mycetophilidae, ♀; C, *Sciara* sp., Sciaridae, frontal view of head; D, same, wing; E, unidentified sp. of Cecidomyiidae. [T. Binder]

39.2F, 14E, 20A, B). A large family, widely distributed throughout the world in both tropical and temperate regions. European workers tend to subdivide it into several different families. However, despite variability in wing venation, it forms a well-knit group, with considerable uniformity in structure and biology; e.g. the constricted base of the abdomen and the larval habitat. Numbers, both of individuals and of species, are highest in wet forest, particularly in temperate climates, but some are quite abundant in the moister parts of open savannah

and heath. Adults, sometimes in enormous numbers, are commonly taken by sweeping low vegetation. They also enter light and Malaise traps, and flight activity seems to be mainly crepuscular or nocturnal. Males of *Keroplatus* (*Heteropterna*) have the remarkable habit of hanging from spider webs, particularly in caves. The larvae are mostly peripneustic, and usually found associated with fungi, either inside the fruiting bodies, or externally in webs or mucilaginous tubes. The more primitive genera include an endoparasite of land planarians, the remark-



able *Planarivora* (Hickman 1965), and a few predators, e.g. the self-luminescent 'glow-worms' (*Arachnocampa*), which trap their prey in hanging mucilaginous threads (A. M. Richards 1960). Glow-worms are not uncommon in certain of our caves, but we have nothing to match the spectacular display seen in the Waitomo Cave, New Zealand.

#### Key to the Subfamilies of Mycetophilidae

1.  $M_{3+4}$  connected with  $M_{1+2}$  by an apparent cross-vein (*m-cu* of some authors, actually the true base of  $M_{3+4}$ ; Fig. 39.20A) ..... 2
- $M_{3+4}$  appearing to fork from CuA, not connected to  $M_{1+2}$  (Fig. 39.20B) ..... 5
- 2(1).  $R_4$  long, almost as long as  $R_5$ , and strongly curved ..... DITOMYIINAE
- $R_4$  short and only slightly curved, or absent ..... 3
- 3(2). Rs and  $M_{1+2}$  fused over a short distance ..... KEROPLATINAE
- These veins not fused, cross-vein *r-m* distinct ..... 4
- 4(3). M with distinct basal section, *m-cu* well basal to *r-m* ..... BOLITOPHILINAE
- Base of M absent, *m-cu* more or less in line with *r-m* ..... DIADOCIDIINAE
- 5(1). Mouth-parts greatly elongate, forming a mosquito-like proboscis; Rs appearing to arise at base of wing; basal part of M absent ..... LYGISTORRHININAE
- Mouth-parts not so; Rs branching from  $R_1$  well beyond base of wing (except in *Allactoneura*), or its base absent ..... 6
- 6(5). Prothorax large, without strong bristles; base of M absent; tibial setulae arranged in lines, fore tibia very short; palpal segment 2 attached subapically on segment 1 ..... MANOTINAE\*
- Without this combination of characters ..... 7
- 7(6). Microtrichia of wing arranged in distinct lines, at least near posterior margin, macrotrichia absent; tibial setulae also arranged in lines; ocelli touching eye margins ..... MYCETOPHILINAE
- Microtrichia of wing irregularly arranged, macrotrichia sometimes present; tibial setulae irregularly arranged, and/or ocelli distant from eye margins ..... SCIOPHILINAE

\* Excluding *Allactoneura*, which we prefer to place in the Sciophilinae.

#### Key to the Families of Orthorrhapha and Aschiza Known in Australia

1. Empodium pulvilliform, i.e. 3 subequal pads below the tarsal claws (Fig. 39.6C); CuA and 1A separate, or meeting at an acute angle rather close to wing margin ..... 2
- Empodium bristle-like or absent, i.e. at most 2 well-developed pads below the tarsal claws, or, if a median pad present, CuA and 1A meeting far from wing margin, not at an acute angle ..... 10
- 2(1). Head very small, eyes holoptic in both sexes; thorax and abdomen greatly inflated; calypters very large; wing venation specialised (Fig. 39.22B) ..... ACROCIDAE (p. 755)
- Not such flies ..... 3
- 3(2). Veins  $R_{4+5}$  and  $M_{1+2}$  fused to form a strong, composite, oblique vein, with 3–5 more or less parallel branches ending before wing apex (2 only in *Nycterimorpha*, which has conspicuously attenuated wing base and 1A close to posterior margin) ..... 4
- Wing venation otherwise ..... 5

Unpublished studies show that all subfamilies are represented in Australia, and the number of species is about the same as in New Zealand; but the fauna more closely resembles that of southern South America in having more genera and fewer species per genus. The only noticeably large genera are *Orfelia* (= *Platyura*), *Mycomya* and *Mycetophila*. Four distinct elements can be discerned. (a) Some 10 to 15 probably endemic genera and subgenera, e.g. *Antriadophila* and the remarkable wasp-mimics, *Nicholsonomyia* and *Pseudalyssiinia*. (b) A distinct, but not well known, Indo-Malayan element mainly in the north, e.g. *Eumanota*, *Allactoneura*, *Epicypta* (= *Delopsis*). (c) A very distinct 'Antarctic' element, e.g. *Australosymmerus* (New Zealand and southern South America), *Paramacrocera* (New Zealand) and *Stenophragma* (southern South America). (d) Cosmopolitan genera, some with species-groups belonging in the two preceding categories. Present information gives the impression that (c) and (d) form the bulk of our fauna, but further collecting in northern areas may modify this view. [Tonnoir 1929; Colless 1970a; Harrison 1966]

#### Suborder BRACHYCERA

Mostly stouter and larger flies than the Nematocera, with the characteristics given in the key. They are clearly derived from bibionomorph-type ancestors, having the fused postphragma and generally similar venational traits. As far as known, they also lack chiasmata in the male, but the X and Y chromosomes form bivalents at spermatogenesis (except in the aberrant Hippoboscidae and a few XO forms). Larvae are generally terrestrial, though many (probably secondarily) aquatic groups are known. It is not yet possible to present keys to the larvae based on Australian material, but reference to J. F. McAlpine *et al.* (1981) may be helpful.

#### Division ORTHORRHAPHA

Separated from the Cyclorrhapha principally by the normal, obtect pupa (enclosed in the unmodified larval skin in Stratiomyidae); also by the form of the male terminalia, which are, at most, only partly rotated and not flexed under the apex of the abdomen (except in Dolichopodidae). It includes the more primitive families of Brachycera, many with a rather generalised venation, with Rs 3-branched and M up to 4-branched. In many families, the adults and/or larvae are predators, or the larvae endoparasites.

- 4(3). Mid and hind tibiae each with 2 ventral apical spurs; antennal segment 3 thick, *ca* 6-annulate; cerci of ♀ 2-segmented (*Exeretonevra*) ..... **Xylophagidae** (p. 755)  
 Tibiae without apical spurs; antennal segment 3 simple and styloform, or terminating in a slender, simple or 3-segmented style; cerci of ♀ unsegmented, sometimes conspicuously long (Fig. 39.22A) ..... **Nemestrinidae** (p. 755)
- 5(3).  $R_4$  and  $R_5$  divergent, the former ending before, the latter far behind, wing apex; cell  $R_4$  relatively short and broad ... 6  
 $R_4$  and  $R_5$  of different conformation; cell  $R_4$  relatively long and narrow ..... 7
- 6(5). Vein 1A strongly sinuate, well separated from CuA; calypters undeveloped (Fig. 39.21G) ..... **Pelecorhynchidae** (p. 753)  
 Vein 1A almost straight, almost always fused distally with CuA; calypters almost always well developed (Fig. 39.21F) ..... **Tabanidae** (p. 754)
- 7(5). Cell  $M_3$  closed; hind femur swollen and toothed on ventral surface ..... **Xylomyidae** (p. 755)  
 Cell  $M_3$  open or absent; hind femur not as above ..... 8
- 8(7). Rs almost always originating opposite or distal to (rarely, slightly basal to) the junction of *m-cu* and CuA; frequently with radial veins crowded anteriorly, discal cell compact (rarely absent), and some branches of M weak or abbreviated distally; prosternum usually connected to propleuron by broad precoxal bridges (Figs 39.21A–D) ..... **Stratiomyidae** (p. 755)  
 Rs originating far basal to junction of *m-cu* and CuA (Fig. 39.21E); radial veins and discal cell otherwise; prosternum isolated, without precoxal bridges ..... 9
- 9(8). Subcutellum distinct; metathoracic spiracle with scale- or tablet-like raised area near posterior rim; 3rd antennal segment reniform, with dorsal arista (*Suragina*) or fore tibia with small but distinct, pale apical spur (*Dasyomma*); wing sometimes banded; palps of ♀ tapering ..... **Athericidae** (p. 753)  
 Subcutellum not developed; spiracle not as above; 3rd antennal segment not reniform and fore tibia without apical spur (but apex encircled with black spines in *Atherimorpha* and *Chrysopilus*); wing at most spotted (*Austroleptis*); palps of ♀ cylindrical or clubbed (Fig. 39.21E) ..... **Rhagionidae** (p. 753)
- 10(1). CuA long, reaching wing margin or joining 1A at less than a quarter of its length back from the wing margin; cell CuP markedly longer than cell M ..... 11  
 CuA absent, vestigial, or short, joining 1A at more than a quarter of its length back from the wing margin; \* cell CuP often little, if at all, longer than cell M ..... 17
- 11(10). Vein  $M_1$  turned forwards to meet  $R_{4+5}$ , which is unbranched; either vein, or both, often sinuous; often with a vein-like fold or thickening ('vena spuria') between Rs and M, and/or terminal branches of M joining to form an 'ambient vein' parallel to margin; antenna with dorsal arista, except in a few wasp-mimics (Figs 39.27A, B) ..... **Syrphidae** (p. 763)  
 Venation otherwise, and/or antenna with terminal style ..... 12
- 12(11). Head at least as large as thorax and subspherical, bounded mainly by the enormous eyes; antenna with dorsal arista;  $R_{4+5}$  unbranched (Figs 39.27C, D) ..... **Pipunculidae** (p. 763)  
 Head not as above, and/or antenna with terminal style, and/or  $R_{4+5}$  branched ..... 13
- 13(12).  $R_5$  and  $M_1$  terminating anteriorly before apex of wing; at most 3 veins terminating posteriorly to apex. [Antenna swollen apically] ..... 14  
 $R_5$  terminating posteriorly to wing apex (except in a few species with  $R_{4+5}$  unbranched and/or with strong, piercing proboscis); almost always with 4 or more veins terminating posteriorly to apex ..... 15
- 14(13). Antennal club petiolate, the preceding segment narrow and elongate; M with only one branch reaching margin posteriorly to wing apex; palps vestigial (Fig. 39.23E) ..... **Mydidae** (p. 758)  
 Antennal club more or less sessile, the preceding segment short; M often with 2 branches reaching or approaching margin posteriorly to wing apex; palps distinct, often expanded apically (Fig. 39.23F) ..... **Apioceridae** (p. 758)
- 15(13). Ocellar tubercle almost always set in distinct notch or depressed area between the well-separated, bulging eyes; face relatively long, more or less vertical, with long bristles forming a 'moustache'-like tuft or line on at least the lower margin; proboscis a stout, horny beak. [Head never subspherical; antennae usually set above centre of anterior surface of head—Figs 39.9C, 23A, B] ..... **Asilidae** (p. 757)  
 Frons at most slightly depressed; eyes often holoptic; face usually short and receding or sharply protruding; proboscis with fleshy labella and/or thin and elongate ..... 16
- 16(15). M with 3 (rarely 2) branches;  $R_{2+3}$  and  $R_4$  often strongly curved distally, meeting costa at about a right angle; often woolly flies (Fig. 39.24) ..... **Bombyliidae** (p. 758)  
 M with 4 branches,  $M_3$  and  $M_4$  usually converging or meeting;  $R_{2+3}$  and/or  $R_4$  less strongly curved; usually sparsely haired flies (Fig. 39.23C) ..... **Therevidae** (p. 756)
- 17(10). Wings rather lanceolate, pointed, with  $R_{4+5}$  terminating at apex and cross-veins confined to base; main veins, except Sc and  $R_3$ , with a dorsal row of black setulae (Fig. 39.26A) ..... **Lonchopteridae** (p. 762)  
 Wing otherwise ..... 18
- 18(17). Radial veins strongly thickened, terminating along with costa at about centre of anterior margin; other veins much weaker, more or less parallel, running obliquely across wing; antenna apparently 1-segmented, globular or

\* Scenopinidae (Fig. 39.23b) and a few Empididae (Fig. 39.25d) have CuA rather long. The latter are immediately recognisable by the humped mesothorax and/or swollen, spinose hind femora; the former are as given in couplet 22.



- discoid, with dorsal arista; head and forwardly-projecting palps usually with strong, spiny bristles (Fig. 39.26E) ..... **Phoridae** (p. 763)
- Not with the above combination of characters ..... 19
- 19(18).  $M_1$  and  $M_2$  incomplete basally; alula and calypters with long barbed hairs; basal half of wing with large area devoid of microtrichia (Fig. 39.26B) ..... **Sciadoceridae** (p. 762)
- Not with the above combination of characters ..... 20
- 20(19). Second antennal segment with conspicuous apical processes on both inner and outer surfaces; Sc fused for most of its length with  $R_1$ , but free at apex; both Sc and CuA+1A reaching margin; CuA curved to meet 1A at about 90°; pre-scutellum well developed (Figs 39.27E, F) ..... **Ironomyiidae** (p. 762)
- Not with the above combination of characters ..... 21
- 21(20). Hind tarsi modified, the basal segment or most segments expanded and flattened; wings broad; cell CuP acute distally (Figs 39.26C, D) ..... **Platypezidae** (p. 762)
- Hind tarsi rarely modified; if modified, cell CuP not acute apically ..... 22
- 22(21). Antenna without apical style or arista, sometimes bifid at tip; CuA not recurved apically, meeting 1A at one-quarter to one-third its length back from wing margin;  $R_{4+5}$  branched;  $M_1$  often curved forward to meet or approach  $R_5$ ; mouth-parts non-predatory (Fig. 39.23D) ..... **Scenopinidae** (p. 757)
- Not with the above combination of characters ..... 23
- 23(22). Rs arising from R very close to level of humeral vein, distal to it by no more than the length of that vein; at most 2 separate veins from apex of discal cell to wing margin; cell M confluent with discal cell (base of  $M_{2+3}$  missing); mouth-parts with strong, opposable labella (Figs 39.3C, 25A, B) ..... **Dolichopodidae** (p. 760)
- Origin of Rs well distal to level of humeral vein, and/or 3 separate veins from apex of discal cell to wing margin; cell M almost always separated from discal cell by base of  $M_{3+4}$ ; mouth-parts usually a piercing beak (Figs 39.25C–E) ..... **Empididae** (p. 759)

### Superfamily TABANOIDEA

Characterised principally by the enlarged, pad-like empodium, which resembles the pulvilli and, with them, forms a triple pad beneath the tarsal claws. The venation is rather generalised (except in Acroceridae), with CuA reaching the wing margin or meeting 1A near its apex. Larvae are aquatic or terrestrial, and some are endoparasites; they have the posterior pair of spiracles approximated on the terminal segment.

The Nemestrinidae and Acroceridae have often been combined with the asiloid family Bombyliidae in a superfamily Nemestrinoidea but, as Hennig (1973) has indicated, the only shared derived characters for all 3 families are the parasitic habits of the larvae and associated hypermetamorphosis. We retain the Nemestrinidae and Acroceridae in the broadly defined and possibly paraphyletic Tabanoidea because of their pulvilliform empodium and, in the larvae, the approximated abdominal spiracles on the terminal segment.

**20. Pelecorhynchidae** (Fig. 39.21G). In Australia the family includes the single primitive genus *Pelecorhynchus*, which was placed in the Tabanidae by early authors, and in the Coenomyiidae by Steyskal (1953). The species are of robust build, 10–20 mm long, usually ornate, with 8-segmented antennal flagellum and hatchet-shaped labella. The females have 2-segmented cerci and reduced mandibles; they are not blood-suckers. The larvae and pupae are more like those of Rhagionidae than of Tabanidae.

The species are confined to cool temperate parts of southern Chile and eastern and south-western Australia. Adults have been taken on *Leptospermum* flowers, or hovering in the air, in the mountains during the summer; a few species appear in coastal districts in the spring. Larvae have been collected in the damp margins of swampy areas, where they feed on earthworms and possi-

bly other soft-bodied animals. They move to drier levels to pupate. [Daniels 1977b]

**21. Rhagionidae** (Leptidae; Fig. 39.21E). A world-wide family of rather small flies (largest Australian species 10 mm long), with sparse hairs, sometimes bristle-like, on body and legs. The primitively 8-segmented antennal flagellum shows progressive reduction to a swollen basal segment and attenuated, often unsegmented style. At least some of the tibiae have apical spurs. The cerci of the female are 2-segmented (1-segmented in *Austroleptis*, which probably requires a separate family); and the male terminalia are basically simple, though showing remarkable variation even within individual genera. The family has been divided recently (see next family below), a process that seems likely to continue.

Most Australian Rhagionidae may be taken by sweeping among vegetation in sheltered, rather damp places. They are particularly common in spring (for *Spaniopsis*, autumn). The species of *Spaniopsis* suck blood, and some can be minor pests in heath and forest. *Austroleptis* sp. visits flowers in W.A. Larvae of *Chrysopilus* are found in damp soil, and *Austroleptis rhyphoides* has been reared from rotting wood. Of the Australian genera, *Austroleptis* and *Atherimorpha* occur also in South America (and *Atherimorpha* in South Africa), whereas *Chrysopilus* and possibly *Spaniopsis* belong to a later northern element. [Paramonov 1962]

**22. Athericidae**. A small, cosmopolitan family, recently excised from the Rhagionidae (Stuckenberg 1973), and probably more closely related to Tabanidae. In Australia it includes some 11 species of *Dasyomma* in the south and one of the almost cosmopolitan *Suragina* in the far northern rainforests. The female of *Suragina* is reputed to suck blood, but the Australian species seems not to attack humans. Larvae are aquatic, and have crochet-tipped pro-legs on each of the 8 abdominal segments.

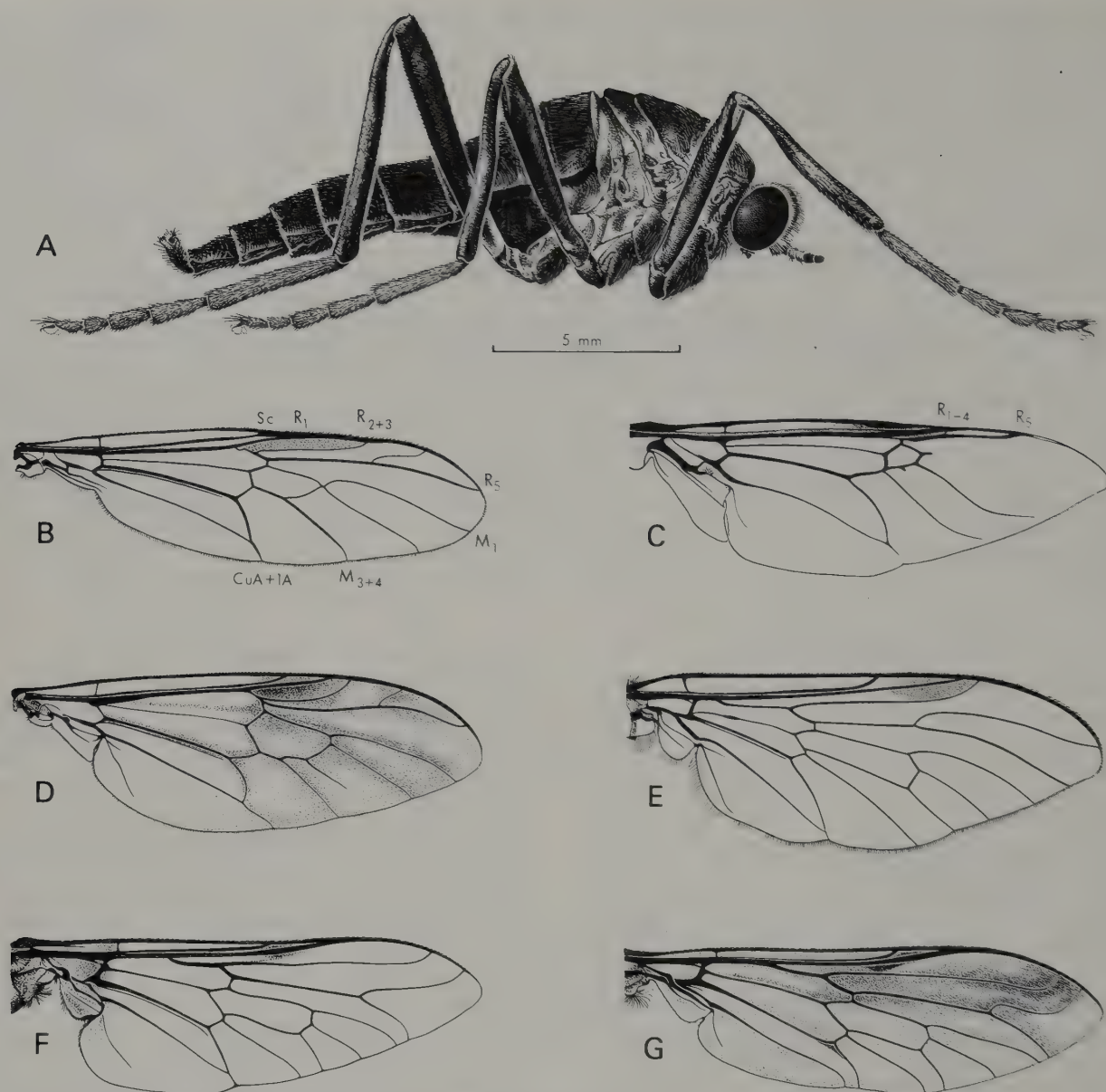


Fig. 39.21 Tabanoidea: A, *Boreoides subulatus*, Stratiomyidae, ♀; B, same, ♂ wing; C, *Odontomyia scutellata*, Stratiomyidae; D, *Exaireta spiniger*, Stratiomyidae; E, *Chrysopilus graciosus*, Rhagionidae; F, *Scaptia auriflua*, Tabanidae; G, *Pelecorhynchus fulvus*, Pelecorhynchidae. [T. Binder]

**23. Tabanidae** (March flies,\* horse flies; Figs 39.2H, 21F). A large and important family, well studied because of its medical and veterinary significance. The Australian species vary from small (6 mm long) to large (20 mm), and all are distinguished by having large eyes, segmented antennal flagellum, strong proboscis and labella, smooth bodies which are more or less hairy and often show dense pleural tufts, at least mid tibiae with apical spurs, and 1-segmented cerci in the female. Division of the family into subfamilies has been based primarily on characters of the terminalia, but most species can be placed correctly on external characters.

\* In Europe and North America, the term 'March fly' is applied to the Bibionidae.

#### Key to the Subfamilies of Tabanidae

1. Ocelli rudimentary or absent; hind tibiae without spurs; antennal flagellum a consolidated basal plate and 4-annulate style ..... TABANINAE
- Ocelli fully developed; hind tibiae with paired apical spurs (occasionally small, rarely absent); antennal flagellum varied ..... 2
- 2(1). Antennal flagellum usually 8-annulate; if with fewer annuli, Sc bare below and  $R_4$  with a strong appendix; frons of ♀ almost always without a shining callus ..... PANGONIINAE
- Antennal flagellum usually with a basal plate and 4-annulate style, occasionally with fewer divisions; Sc usually setulose below;  $R_4$  usually without appendix; frons of ♀ almost always with a shining callus, which is occasionally linear ..... CHRYSOPSINAE



PANGONIINAE, CHRYSOPSINAE and tribe Tabanini were reviewed by Mackerras (1956–71). The remaining TABANINAE (Diachlorini) comprise one species of *Lissimas*, about 35 of *Cydistomyia*, and about 75 of *Dasybasis* (D. Spratt, pers. comm.).

Most of the Australian species suck blood, but some species of *Scaptia* (Plate 5, N) appear to be exclusively flower-feeders, and the most primitive Pangoniini seem to live obscure lives among low vegetation; the females of a few of these have atrophied mandibles. The commonest genera in southern Australia are *Scaptia*, thickset Pangoniinae with hairy eyes, and *Dasybasis*, hairy-eyed Tabaninae with bare basicosta and  $R_4$  appendiculate; in the north, *Tabanus*, with setulose basicosta, *Cydistomyia*, bare-eyed Tabaninae with bare basicosta and  $R_4$  without appendix, and *Lilaea*, *Cydistomyia*-like Chrysopsinae, are common. Some of the blood-sucking species are pests of humans and stock, and one northern species is known to produce sensitisation, with severe reaction to subsequent bites. However, none of our species occurs in such vast numbers as those of the subarctic zone of the Northern Hemisphere. Tabanidae transmit loiasis of humans in Africa and trypanosome infections of stock in the Old World tropics; but in this country, disease transmission is, as far as known, limited to a filaroid nematode of kangaroos and wallabies.

The breeding places of the Australian species are extremely varied: in classical situations among floating vegetation in open swamps; in the mud of rivers; in more or less damp soil, among rotting vegetation; in dry or beach sand; or even in rot-holes in the trunks of *Casuarina*. The more primitive genera have a predominantly southern distribution in Australia, and are related to groups in New Zealand, South America and South Africa. Some old genera and subgenera, however, have a more northern distribution, and they are connected with corresponding African groups by a discontinuous band of species that extends around the Indian Ocean and also into the Pacific. The most highly evolved genera (*Chrysops*, *Tabanus*) appear to have become distributed from northern centres of evolution along with the eutherian mammals. [Mackerras 1956–71]

**24. Stratiomyidae** (Figs 39.6C, 21A–D). A cosmopolitan family, including a wide range of forms, from among the most primitive in the suborder to others that are highly specialised; but most members can be recognised by the characteristic venation. The antennal flagellum is often elongate, and usually annulate; the proboscis short and fleshy; the tibiae without apical spurs (except in some Beridinae and all Antissinae); the cerci of the female 2-segmented; and the male terminalia of rather simple form.

The family has not yet been studied critically in this country, but it can be seen that, as in the Tabanidae, the older elements show relationships with South America, and the more specialised ones with the Oriental region. The elongate, soft-bodied Chiromyzinae, including *Boreoides* which has apterous females (Fig. 39.21A), are not uncommon in the south-east, especially in higher country. *Exaireta spiniger* is common in gardens. The slightly metallic species of *Odontomyia* are the most common

representatives of the family; they may be collected in numbers in any swampy area, both coastal and montane, settled on low vegetation or hovering in the air over open patches. A few genera contain some remarkably good wasp mimics (Plate 6, I; see also Nicholson 1927). Larvae of Stratiomyidae are distinctive, being elongate, somewhat flattened, with permanently exerted heads, and densely shagreened cuticles. Some are aquatic, but many are found in damp soil or rotting vegetation. The pupa remains enclosed within the last larval skin, a characteristic shared only with Xylomyidae in the superfamily. *Inopus rubriceps*, which breeds abundantly in soil, is a serious pest of pastures and sugar cane in Qld. [G. H. Hardy 1959; Daniels 1979]

**25. Xylomyidae** (Solvidae). A small family, of scattered world distribution, related to Stratiomyidae, and distinguished in Australia from the Rhagionidae by the swollen hind femora, closed cell  $M_3$ , and complex, strongly down-turned male terminalia. Our single species, *Solva laeta*, occurs in North Qld and New Guinea. [Daniels 1977a]

**26. Xylophagidae** (Coenomyiidae). Typical soil-dwelling xylophagid larvae (see, e.g., J. F. McAlpine *et al.* 1981) have been found in Tas. (M. Williams, pers. comm.), but no adults have been reared. It seems likely that they will be found to belong to some genus currently placed in another family. *Atherimorpha* and *Exeretonevra*, currently in Rhagionidae and Nemestrinidae respectively, seem likely candidates. In any case, we propose on general grounds to transfer the latter genus to this family. Despite some resemblance to Nemestrinidae in wing venation, *Exeretonevra* is clearly misplaced there; but Nagatomi's (1977) erection of a monotypic family seems to us premature. Adults of *Exeretonevra* occur in highland areas from northern N.S.W. to Tas., and may be locally common on vegetation near streams. Their flight is weak and slow, and they appear reluctant to fly. [Paramonov 1953b; Nagatomi 1977]

**27. Nemestrinidae** (Fig. 39.22A). This family is easily recognised by the wing venation. Most are large to medium-sized, compactly built flies, usually hairy but never bristly; typically the abdomen is conical, the 6th and subsequent segments in the female forming a tubular, retractile 'ovipositor' with a pair of strikingly elongate, 1-segmented cerci.

The medium-sized to large, often rather ornate species of *Trichophthalma* are much the most abundant. They are most often taken when feeding on blossom or hovering motionless over open sunny patches, darting away when disturbed, but usually returning quickly to the same spot. The larvae are parasitic, and those of *Trichopsidea oestracea* are found in grasshoppers. Of the 6 genera definitely recognised in Australia, *Cyclopsidea* is a specialised endemic element, *Trichophthalma* is shared with southern South America, and the others are recent derivatives from the north. [Paramonov 1953b]

**28. Acroceridae** (Cyrtidae; Fig. 39.22B). A small family of grotesquely inflated flies, remarkable for having the eyes holoptic in both sexes (apparently fused in *Pterodontia*), contact being below the long antennae in

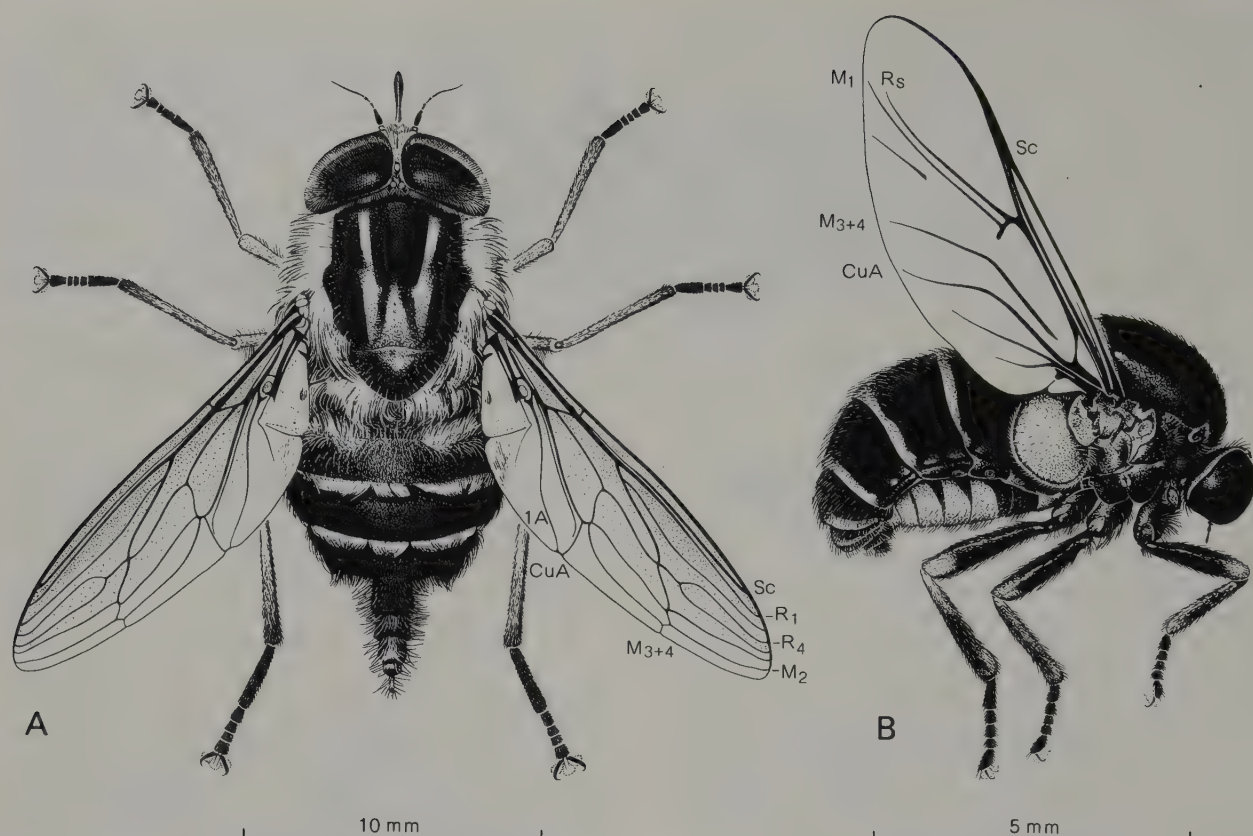


Fig. 39.22 Tabanoidea: A, *Trichophthalma laetilinea*, Nemestrinidae; B, *Ogcodes basiliis*, Acroceridae.

[T. Binder]

*Panops* and the wasp-like *Leucopsina* (Plate 6, Y), and above the very short antennae in *Pterodontia* and *Ogcodes*. Consequently, the sexes cannot usually be distinguished without examining the terminalia, which are also considerably modified, with those of the male rotated from 90 to 180°. Most of the species are rare, but *Ogcodes* is sometimes taken in considerable numbers. The early stages are parasitic in spiders. Eggs of *Ogcodes* are often laid profusely on wires, fences, clotheslines and even radio-telescopes; but practically nothing is known of life histories in Australia. *Leucopsina*, *Panocalda* and *Mesophysa* are endemic, *Panops* occurs also in South America, while *Pterodontia* and *Ogcodes* are cosmopolitan. [Paramonov 1957; Neboiss 1971]

### Superfamily ASILOIDEA

Generally similar to the Tabanoidea, but empodium bristle-like, reduced, or absent. The larvae are mostly terrestrial, and many are predatory, or, in the Bombyliidae, endoparasites. Their posterior abdominal spiracles are placed laterally on the penultimate segment.

**29. Therevidae** (Fig. 39.23c). A cosmopolitan family of flies of moderate to small size, often with prettily patterned wings and/or silvery pubescent markings on the body. Many species show marked sexual dimorphism. Some resemble small Asilidae, others Rhagionidae or Apioceridae, while many are wasp-mimics (Plate 6, W). The antennae are sometimes very distinctive, with a

greatly elongate or thickened scape. Adults frequent a wide variety of habitats, often in rather dry situations, e.g. sand dunes or beaches. *Agapophytus* is common on tree trunks and *Ectinorhynchus* can often be seen hovering above and among shrubs. Little is known of their habits; they are reputed to be predacious, but this seems unlikely. The larvae are smooth and vermiform, with a rather well developed head; the abdomen is secondarily divided into some 16 apparent segments, and terminates in a pair of tiny pseudopods. They are found mainly in sand or soil, are predacious, and are occasionally reported to give a painful bite (English 1950). The prepupal larva lies in the soil in a characteristically curved attitude.

Our genera show an extraordinary degree of endemism. Of those so far recognised (many are still undescribed), all but 2 are so far recorded only from Australia. *Anabarhynchus*, one of Australia's commonest genera, is also dominant in New Zealand, and it (or close relatives) also occurs in South America. *Ectinorhynchus* is also recorded from New Zealand. These two genera appear to be rather ancient elements, of the 'Antarctic' type, but the provenance of other genera is obscure. The large number of endemic genera reflects the great structural diversity found within the world fauna. This is perhaps related in some fashion to the wasp-mimicking habit, and tends to obscure relationships. However, there is a strong indication of a perhaps ancient radiation in Australia from ancestors whose origins are no longer clear. [Mann 1928-33; Paramonov 1950a]



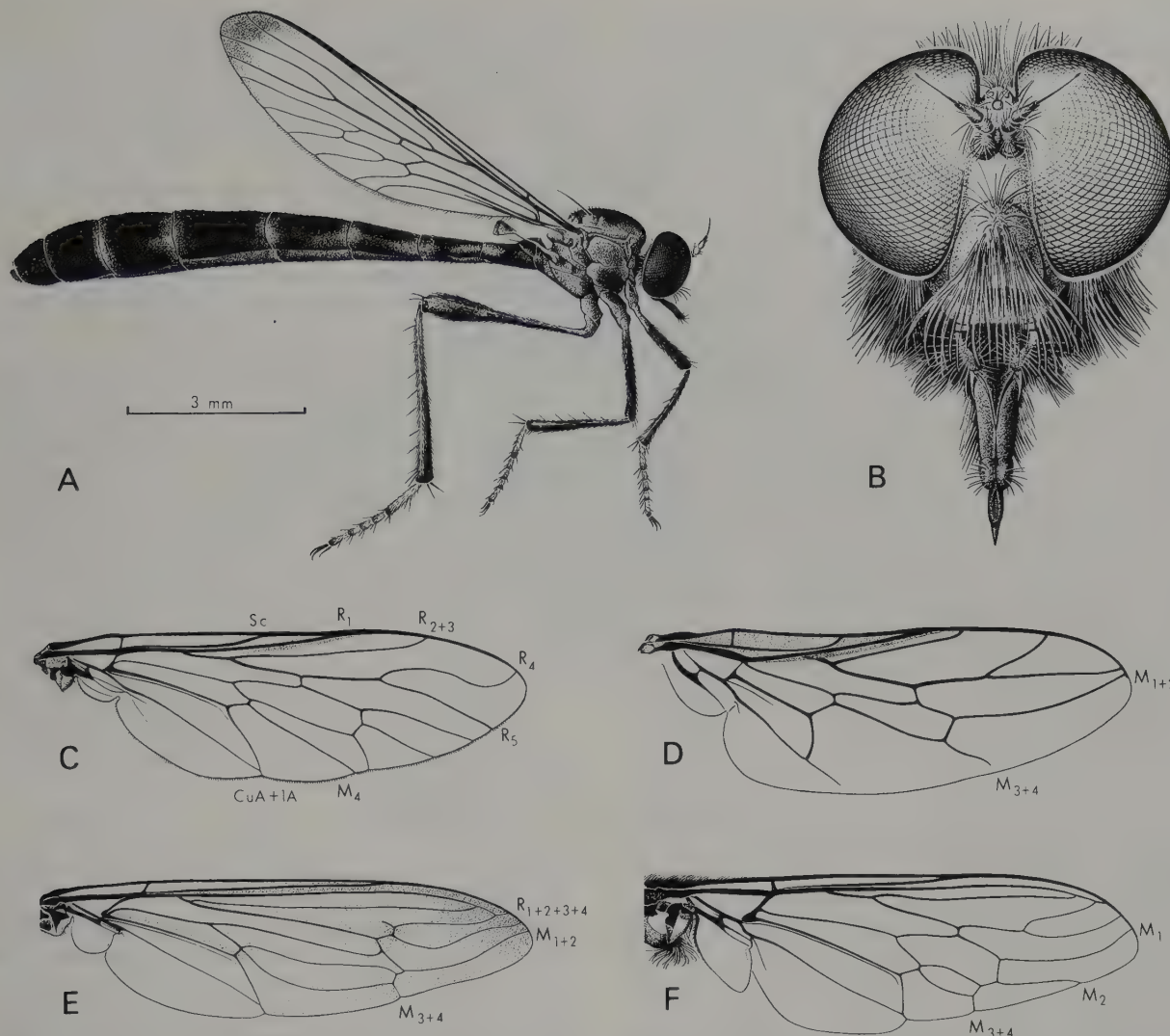


Fig. 39.23 Asiloidea: A, *Leptogaster* sp., Asilidae, ♀; B, *Neoaratus hercules*, Asilidae, head, anterior view; C, *Anabarhynchus calceatus*, Therevidae; D, *Scenopinus glabrifrons*, Scenopinidae; E, *Miltinus viduatus*, Mydidae; F, *Apiocera asilica*, Apioceridae. [T. Binder]

**30. Scenopinidae** (window flies; Fig. 39.23D). A small but widespread family of rather small, dark flies; 6 genera are known from Australia, 2 of them apparently endemic. The bulk of our fauna (70 out of 83 species) has been described since 1969; many species are known from single specimens, and much of the fauna may still remain to be discovered. Adults are uncommon; those of the rarer genera have been mostly swept from vegetation, but some *Scenopinus* spp. are commonly collected on windowpanes. The larvae have a secondarily segmented abdomen, like small Therevidae. They occur in rotting vegetation, and have been found in bird nests; in *Scenopinus* at least, they are probably predacious. *S. fenestralis* is said to breed in houses, preying on larvae of moths and carpet beetles, which explains why this European species has now spread to many countries of the world. [Kelsey 1987]

**31. Asilidae** (robber flies; Figs 39.9C, 10B, 23A, B). A very large family of predatory flies. The shape of the

head, with its prominent, well separated eyes, is very characteristic, while most species are bristly, with strong legs, short, stout thorax, and long, but stout, tapering abdomen; though some have the abdomen narrow and elongate. The venation is rather generalised, with both R and M 4-branched, specialisation being towards apical fusion of R<sub>2+3</sub> with R<sub>1</sub>, M<sub>3</sub> with M<sub>4</sub>, or CuP with 1A. Most asilids are of moderate size, but there are tiny species of *Stichopogon* with wing length of only 1.7 mm, while *Phellus* and *Blepharotes* include the giants of Australian Diptera, with wing-spans up to 75 mm. Some species, particularly in the Dasypogoninae (*s.l.*), have orange or yellow markings on wings or body (Plate 6, H, L), and are effective mimics of sphecids and vespids wasps.

The adults, which live mainly in open forest country, are aggressive predators, feeding particularly on Diptera and Hymenoptera, but attacking almost all insects, including dragonflies; even the hand of the collector is not immune! The prey is usually caught on the wing and

held by the powerful legs; neurotoxins and proteolytic enzymes are injected, and the body juices sucked out via the sharp proboscis (Kahan 1964). Eggs are laid in the soil, or attached to foliage or bark; many Asilinae oviposit in seed-heads of grasses. The larvae are cylindrical, elongate, tapered at each end, and with a small, distinct head. They live in soil or rotting wood, etc., and, although often regarded as predacious, at least some species are not so.

Four subfamilies may be recognised (from 2 to 6 or more, according to various authorities). The ASILINAE, with 1-segmented palp, slender antennal style, and cell  $R_1$  closed and apically petiolate, are well represented here by species of *Colepia*, *Zosteria*, *Cerdistus*, *Ommatius* and others, including the giant species of *Blepharotes*. The LEPTOGASTERINAE, which differ in having cell  $R_1$  open to the costal margin, include, in Australia, only the delicate, elongate species of *Leptogaster*. The LAPHRIINAE and DASYPOGONINAE have 2-segmented palps and a thickened terminal style, or none, on the antenna. The former, with cell  $R_1$  closed, comprise mainly the relatively stout, usually shiny metallic, species of *Laphria* (Plate 5, M), some of which are wasp-mimics. The Dasypogoninae, with cell  $R_1$  usually open, or with a strong terminal spine on the fore tibia, are the dominant group, including over half of the known Australian fauna. *Bathypogon* is possibly the most widespread and diverse genus in the family. Generally, the Australian asilid fauna is very characteristic, with some 80% of its genera (e.g. *Chrysopogon*) endemic. Most of the remainder are more or less cosmopolitan, e.g. *Laphria* and *Leptogaster*, but there are some notable links with the Neotropical region, e.g. *Eccritosis*, *Bathypogon* and the tribe Phellini. [Hull 1962 (references to papers by Ricardo, Hardy and Paramonov); Paramonov 1964a–c; Clements 1985; Daniels 1975–87]

**32. Apioceridae** (Figs 39.2G, 23F). A small family of mostly rather large flies, somewhat resembling Asilidae and Therevidae, but rather short winged, with  $R_4$ ,  $R_5$  and  $M_1$  all turned up distally to end before the wing apex. The abdomen is usually broad at the base, tapering distally, and often has grey markings. Adults are strong, noisy fliers, and occupy a wide range of habitats, from sea beaches and desert to forests at high altitudes; at least half of our known species are associated with relatively arid conditions. Although essentially flower-feeders, they are usually found resting on the ground. The immature stages are known only for *Apiocera maritima*, which breeds in beach sand (English 1947). Its larva is possibly carnivorous, somewhat resembling an asilid, but with a long penultimate abdominal segment.

The world fauna has a curiously disjunct distribution, possibly due to considerable extinction during past epochs. Some two-thirds of known species are Australian, and none is known from the Palaearctic Region or New Zealand. There are 2 Australian genera; *Apiocera* (68 spp.) with  $M_1$  ending on the wing margin, and the endemic *Neorhaphiomydas* (7 spp.) with both  $M_1$  and  $M_2$  fused apically with the radial veins. The latter has a close relative in Chile. [Paramonov 1953c, 1961c]

**33. Mydidae** (Figs 39.2I, 23E). A small family of hand-

some flies, of moderate to very large size (the Neotropical *Mydas heros* is one of the world's largest flies). They bear a superficial resemblance to Asilidae and Apioceridae, but are recognisable by the long, clubbed antennae and the venation. Many are wasp-mimics, e.g. *Diachlistus auripennis*, which resembles the large, orange-winged Pompilidae. Mydids are not very common, but occupy a wide variety of habitats, usually in open country. *Miltinus viduatus* is widespread, found both in the humid eastern regions and the dry interior, but most species seem to be much more restricted in range and habitat. Adults may be taken visiting flowers, but it is thought that at least some are predators. The larvae are said to be predacious, and are recorded in other countries as feeding on beetle larvae in rotting wood; they have been little studied in Australia.

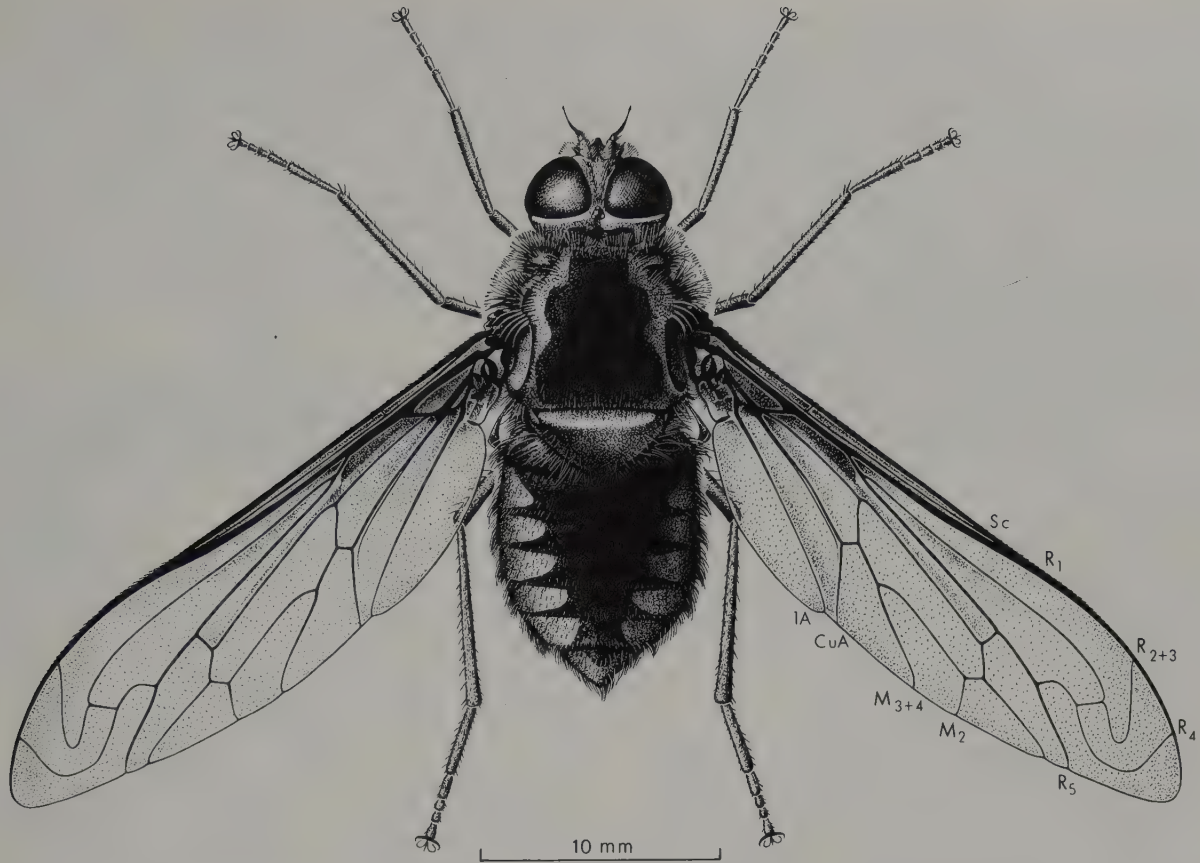
The Australian fauna has a striking distribution, resembling that of the Apioceridae. There are 3 genera, all endemic: *Anomalomydas* with anal cell widely open, *Diachlistus* with  $M_2$  present, and *Miltinus* with  $M_2$  absent. *Diachlistus* is found in most states, but best represented in southern Qld by 6 of the 12 known species. *Miltinus*, however, is found mainly in the more arid areas, occurring around, and presumably in, the desert interior. The 2 species of *Anomalomydas* are known only from S.A. and W.A. The world fauna generally seems to be an old one, adapted to hot and/or arid climates, and has probably suffered much extinction due to climatic changes. [Paramonov 1955b, 1961b]

**34. Bombyliidae** (Fig. 39.24). A very large, cosmopolitan family of usually stoutly built flies, of small to large size, and mostly with very characteristic venation. In Australia, wing-spans vary from over 70 mm in *Comptosia lateralis* down to some 3.5 mm in the tiny *Glabellula australis*. A few, e.g. *Systropus flavoornatus* (Plate 6, S), are remarkable wasp-mimics; in others, mostly members of the subfamily Bombyliinae, the stout, hairy body and long, thin proboscis, together with their flight habits, have earned them the vernacular name 'bee flies'.

The adults favour warm, sunny localities. Although occurring throughout the continent, they form a particularly characteristic element of the fauna in the more arid climates. Most have a strong, hovering flight, and are commonly taken hovering above, or resting on, blossom or patches of bare earth. Females in most subfamilies have the extraordinary habit of gathering sand-grains in a special chamber at the apex of the abdomen—apparently to use as a coating on the eggs (Mühlenberg 1971). The larvae are believed to be parasites in eggs or larvae of other insects. Little is known about Australian species, but some are known to parasitise Hymenoptera and Lepidoptera, and several have been reared from Diptera (Asilidae, Therevidae and Mydidae) and Neuroptera. Nothing appears to be known of the larval biology of our dominant genus, *Comptosia*, but it is thought that some species of this and other genera attack the egg-masses of grasshoppers and locusts.

Fourteen subfamilies are known to occur in Australia; less than half of the species have been described but several authors are currently studying the family. The dominant subfamily, with some 200 species (55 described), is



Fig. 39.24 *Comptosia lateralis*, Bombyliidae, ♀.

[T. Binder]

the LOMATIINAE, in which the occiput has a deep central cavity, the posterior eye-margins are indented, and Rs forks well before *r-m*. Most species belong to the great genus *Comptosia*, an 'Antarctic' element, closely related to *Lyophlaeba* of South America (Evenhuis 1982). The EXOPROSOPINAE, which resemble the Lomatiinae, but with Rs forking close to *r-m*, are well represented, mainly by the cosmopolitan genera *Ligyra*, *Exoprosopa* and *Villa*. The first two belong to the northern element, but *Villa* is abundant in Tas., where the other two are rare or absent. The ANTHRACINAE, another northern element, are represented by some 20 species of *Anthrax*, which differ from the Exoprosopinae in lacking a basal tooth on the tarsal claw and having a pencil of hairs at the tip of the antenna.

The subfamily BOMBYLIINAE includes some 80 Australian species, principally of *Staurostichus*, with smaller numbers of *Sisyromyia*, *Meomyia* and other genera. Most are stout and hairy, with long, slender proboscis and 1-segmented palp; the abdomen is broad and oval, the tibiae spinose, and, in many, vein  $M_1$  meets  $R_5$  before the wing margin. All the genera are endemic, but the subfamily as a whole is of northern origin. The PHTHIRIINAE (*s.l.*) form a smaller, rather heterogeneous group, somewhat resembling the Bombyliinae, but with smooth tibiae, or 2-segmented palp, or elongate body; *Geron* has M only 2-branched. *Acreotrichus*, *Australiphthiria* and *Marmosoma* are endemic, *Thevenemyia* may be 'Antarctic' in origin, whereas *Geron* is apparently of northern origin.

The rest of the Australian fauna consists of a few species in the primitive, wasp-mimicking SYSTROPINAE and the extremely rare TOXOPHORINAE; several in the endemic *Neosardus* (CYLLENIINAE); and a few small to minute species of CYRTOSIINAE, which have  $R_{4+5}$  unbranched. [Roberts 1928–29; G. H. Hardy 1933b, 1941; Paramonov 1950b, 1951, 1953a, 1967; Bowden 1971a,b; Hall 1969; Evenhuis 1979a,b, 1983, 1986; Yeates 1988a,b]

### Superfamily EMPIDOIDEA

Characterised principally by the shortening of CuA, which is usually recurved to end in the basal half of 1A, or may even be obsolescent. The male terminalia are generally very complex structures, partly rotated and asymmetrical in hybotine Empididae, and circumverted in the fashion typical of the Cyclorrhapha in the Dolichopodidae. As far as is known, most adults and larvae are predatory, and the larvae are terrestrial or aquatic.

**35. Empididae** (Figs 25C–E). A very large family of flies, of moderate to minute size. Despite considerable diversity, they form a clear-cut group, recognised mainly by the venation and the general predatory appearance. In most genera, the proboscis is elongate to some extent and adapted for piercing, though a few have 'chewing labella', as in the Dolichopodidae. The male terminalia are often highly complex, and, in the Tachydromiinae and Hybotinae, asymmetrical, and the legs may be greatly

modified; e.g. the extraordinary mid legs of males of *Ceratomerus* (= *Tomia*) (Paramonov 1961a). Probably most adults are predacious on smaller arthropods. They frequent moist places, particularly along streams, and are commonly collected by sweeping vegetation; many are taken in light traps, and a few are found visiting flowers. Species of *Hilara* are often to be seen dancing swiftly close to the surface of small ponds, whereas some other genera form dancing swarms in the air. However, the Tachydromiinae and Hemerodromiinae are mainly terrestrial and rarely fly. Swarms consist largely of males, and swarming forms part of their often complex mating activity; some have very elaborate courtship behaviour, offering captured prey or a bubble of frothy secretion as a lure to attract females (reviewed by Chvála 1983). Little is known of the larvae, which appear to be predacious; some are recorded from the soil or decaying vegetation (including leaf litter and wood), whereas others are aquatic (K. G. V. Smith 1969).

Five subfamilies are here recognised, the Clinocerinae being included in the Hemerodromiinae and the Ocydromiinae in the Hybotinae. Some are now treated as families by some European workers.

#### Key to the Subfamilies of Empididae

1. Discal cell absent (Fig. 39.25E);  $R_{2+3}$ ,  $R_{4+5}$ ,  $M_{1+2}$  and  $M_{3+4}$  all unbranched; cell CuP absent, or, if present (*Platypalpus*), mid legs raptorial; fore legs not raptorial ..... TACHYDROMIINAE
- Discal cell usually present, and/or one or more of the above veins branched, and/or fore legs raptorial ... 2
- 2(1). Third antennal segment very large, with 2nd segment inserted thumb-like on its inner side towards the base; cell CuP indistinct ..... CERATOMERINAE
- Antenna not as above; cell CuP often complete and distinct ..... 3
- 3(2). Wings relatively long and narrow, anal lobe not developed or very weak; thorax usually rather elongate, mid coxae vertically beneath scutellum or postnotum; fore legs often raptorial, with elongate coxae and strong spines on underside of femur ..... HEMERODROMIINAE
- Wings relatively broader, with distinct, rounded anal lobe, and/or thorax more globular in shape; mid coxae vertically beneath scutum; fore legs rarely raptorial ..... 4
- 4(3). Distal part of CuA not in line with *m-cu*, and/or not strongly recurved into 1A (Fig. 39.25D);  $R_{4+5}$  unbranched, and, in known Australian species, M with at most 2 branches reaching margin of wing; cell CuP sometimes longer than cell M ..... HYBOTINAE
- Distal part of CuA usually more or less in line with *m-cu* and strongly recurved into 1A (Fig. 39.25C); M with 3 branches reaching margin and/or  $R_{4+5}$  branched; cell CuP shorter than cell M ..... EMPIDINAE

At least half of the Australian species await description, but the family seems most abundant in the cooler southern and eastern states, though Tachydromiinae are

very common in the north. All subfamilies are represented, dominated by the Empidinae, with many species in the large world-wide genera *Empis* and *Hilara*. There is a distinct 'Antarctic' element, e.g. *Ceratomerus*, *Proagomyia*, *Asymphyloptera* and *Atrichopleura* (one species closely resembling the South American *A. caesia*); while a little-studied northern element is represented by various species of Hybotinae and Tachydromiinae. The curious genus *Microphorella* is apparently annectant with the Dolichopodidae (Colless 1963). [Collin 1928; G. H. Hardy 1930, 1934; Malloch 1930; K. G. V. Smith 1969; Chvála 1983]

**36. Dolichopodidae** (Figs 39.2I, 3C, 8D, 9E, 25A, B). A large family of flies, apparently a specialised offshoot of the Empididae. Most are of rather slender build and moderate to small size; *Heteropsilopus cingulipes* (Fig. 39.25A) expands about 17 mm, but most are much smaller. The thoracic integument is usually metallic, and often bluish, greenish or bronzy in hue. In many genera, the venation resembles that of the muscoid families. The mouth-parts are predacious, but developed in an unusual fashion: only rarely elongate, rather fleshy, with the labella forming a pair of longitudinally opposed lips, their edges sharp and sometimes set with small spines (Fig. 39.3C). The antennae usually have a long, fine arista, but are sometimes strikingly modified; e.g. *Syntormon*, which shows a remarkable parallel with the empidid *Ceratomerus*. Some species show strong sexual dimorphism, with bizarre modifications of the male wing, legs and antennae. Adults are very common, and often to be seen on foliage, tree trunks, etc., or on mud or sand beside bodies of water, fresh or salt; species of *Hydrophorus* are water-striders. An unusually rich fauna is found on smooth-barked tree trunks, which are used as leks or for mating assemblies. The Sciapodinae are common in exposed, sunny situations, but others, e.g. *Sympycnus*, are largely restricted to wet forest. All seem to be predacious; some prey on smaller arthropods, and certain Sciapodinae are useful predators on pest species of aphids; many others probably feed on small oligochaete worms in mud or sand. The maggot-like larvae resemble those of the Empididae; exotic species have been reported from mud, rotting vegetation and under bark, and at least some are predacious.

The Australian fauna is fairly well known in outline, though not in detail. Thirty six genera are recorded, with about 60% of described species falling in two dominant subfamilies. The SCIAPODINAE are mostly rather large, brilliant green or blue species, with excavated frons and  $M_{1+2}$  usually branched; *Heteropsilopus cingulipes*, *H. ingenuus* and *Sciapus connexus* are common widespread species, the two last with banded wings. The SYMPYCINAE are mostly small, semi-metallic species, including *Sympycnus* (usually dark and lacking acrostichal bristles) and *Chrysotimus* (often green, with biserial acrostichals and a depressed area in front of the scutellum). Seven other subfamilies are represented. There is a large element of oriental origin, e.g. *Neurigona*, *Paraclius* and *Medetera*, which are found mainly in northern and eastern areas. The Sciapodinae are also



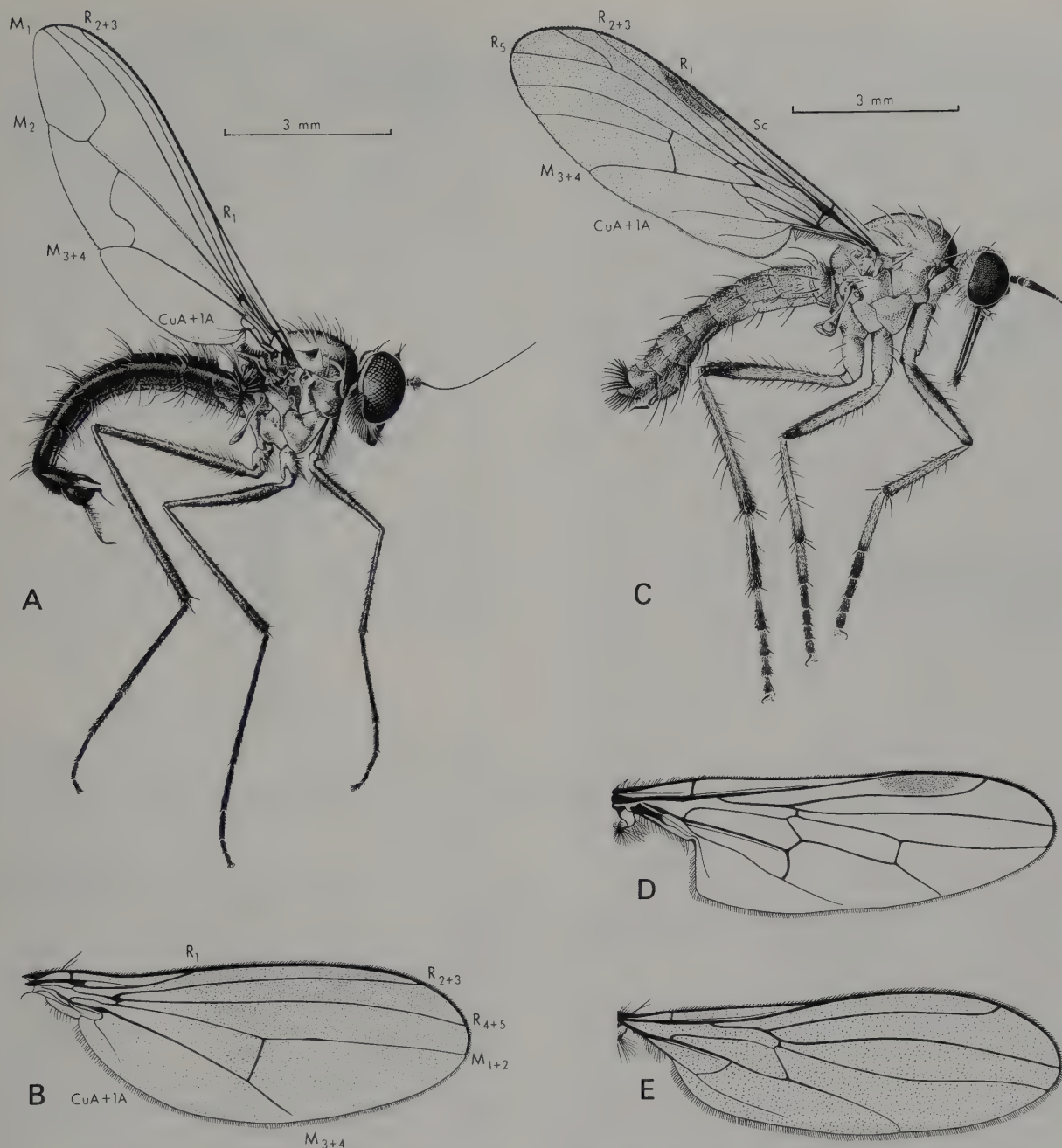


Fig. 39.25 Empidoidea: A, *Heteropsilopus cingulipes*, Dolichopodidae, ♂; B, *Sympycnus allectorius*, Dolichopodidae; C, *Empis* sp., Empididae, ♂; D, *Syneches* sp., Empididae; E, *Platypalpus* sp., Empididae. [T. Binder]

essentially tropical although *Heteropsilopus* and *Parentia* have classical Bassian distributions. On the other hand, *Sympycnus* may be an 'Antarctic' element, being a dominant genus in the faunas of New Zealand and southern South America, although also distributed well into the tropics to the north of Australia. [Bickel 1987a–c]

#### Division CYCLORRHAPHA

Characterised principally by the coarctate pupa, which remains permanently pharate within a puparium formed from the larval skin; also by the circumverted male terminalia, which are flexed forwards ventrally beneath the

preceding segments and usually lack recognisable coxites. The larvae are generally of the acephalic 'maggot' type and mainly terrestrial, typically in decaying organic matter, though true aquatic forms occur; many are phytophagous, parasitic or predacious (Ferrar 1988).

#### Series Aschiza

A rather heterogeneous assemblage of families, distinguished mainly by the absence of the ptilinal fissure but the presence of circumverted male genitalia. Some families show features annectent with the Orthorrhapha, and all are included in the key on p. 751.

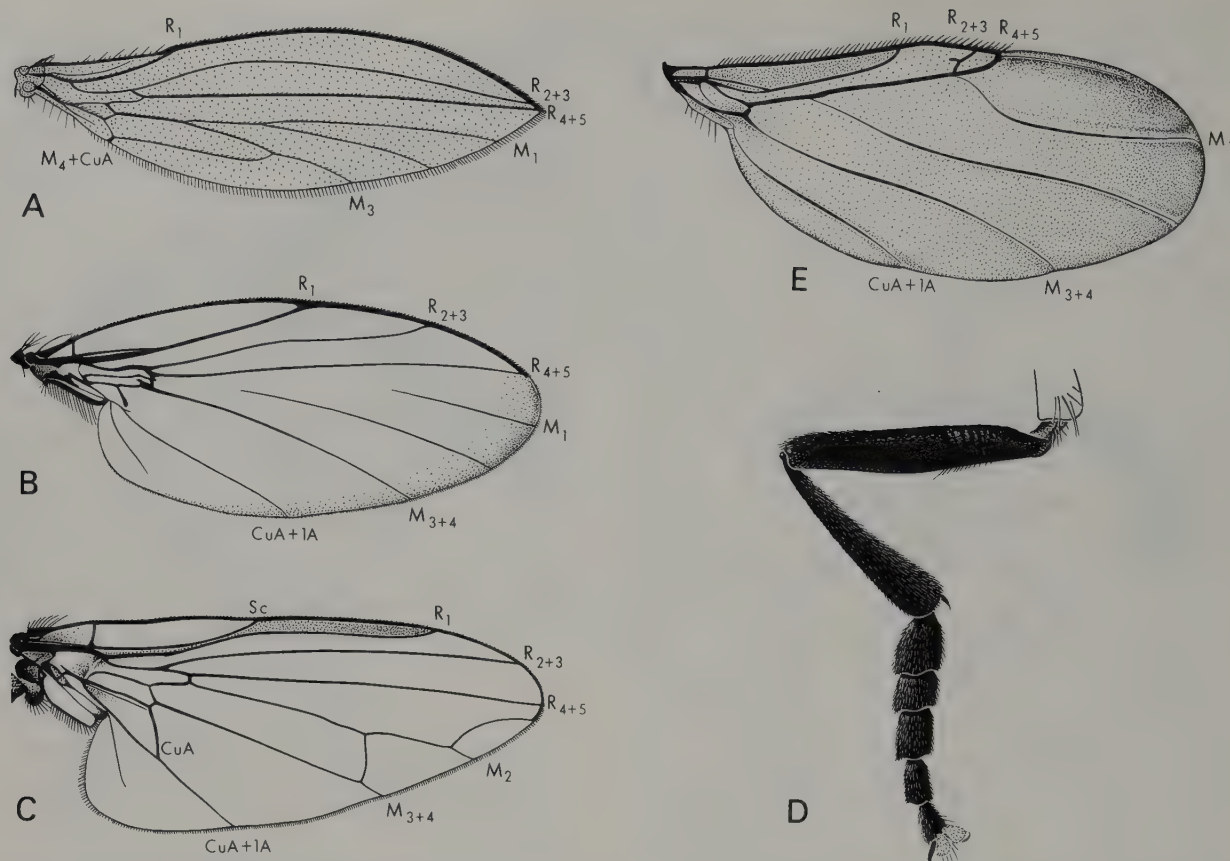


Fig. 39.26 Lonchopteroidea and Phoroidea: A, *Lonchoptera furcata*, Lonchopteridae; B, *Sciadocera rufomaculata*, Sciadoceridae; C, *Platypeza* sp., Platypezidae; D, same, ♂ hind leg; E, unidentified sp. of Phoridae. [T. Binder]

### Superfamily LONCHOPTEROIDEA (Anatriata)

The most significant characters are found in the immature stages. The larvae retain maxillae and a vestigial head capsule which is not withdrawn into an atrium, yet the pupa is coarctate as in the higher groups of Cyclorrhapha.

**37. Lonchopteridae** (Musidoridae; Fig. 39.26A). Slender flies with well developed bristling on head and thorax and characteristic wing venation; CuA + 1A are joined distally to  $M_4$  in the female only. The only Australian species, *Lonchoptera furcata* (= *dubia*), of this monogeneric family has perhaps been introduced from Europe or America. It reproduces parthenogenetically (Stalker 1956) and males are extremely rare. The larvae live in decaying vegetation.

### Superfamily PHOROIDEA

Adults and larvae resemble those of the next superfamily in many characters, but adults usually have a terminal arista and cell CuP more or less shortened. The pre-abdomen of the male consists of 6 segments, with the postabdomen circumverted, at least in Sciadoceridae and presumably in the other families.

**38. Ironomyiidae** (Figs 39.27E, F). A very small family, with only 2 modern species (of *Ironomyia*, both endemic, one undescribed). *I. nigromaculata* occurs in forest in south-eastern Australia and has been reared from

leaf litter containing lepidopterous larvae. Another fossil species is known from Cretaceous amber. Nothing is known of their biology. [J. F. McAlpine 1973]

**39. Platypezidae** (Clythiidae; Figs 39.26C, D). Rather small flies, somewhat resembling Phoridae in life, due to the humped thorax and jerky method of running. The hind tarsi are always modified, and often conspicuously compressed and dilated. The larvae are ovoid and flattened, with lateral projections on the segments; they live in fungi so far as known. *Platypeza* (s.l.), with  $M_{1+2}$  forked beyond the discal cell, is the commonest genus. *Agathomyia* is similar, but with  $M_{1+2}$  simple. The smoke fly, *Microsania australis*, may be seen flying in the smoke of camp fires in large numbers in cool localities; it has very weak venation and the discal cell open. [Tonnoir 1925; Collart 1938; Kessel and Maggioncalda 1968]

**40. Sciadoceridae** (Fig. 39.26B). The venation is intermediate between that of the Platypezidae and the more specialised venation of the Phoridae. The male has only one vestigial sclerite between abdominal segment 6 and the terminalia, which are not deflexed. The Australian species, *Sciadocera rufomaculata*, occurs in wet forest from Tas. to Central Qld, and also in New Zealand. The only other recorded species of the family are the recent *Archiphora patagonica* from Patagonia and *A. robusta*, a fossil from Baltic amber (Hennig 1964). *S. rufomaculata* has been reared in the laboratory (Fuller 1934) and may



be a carrion-breeder, but the early stages have not been found in the field. [J. F. McAlpine and Martin 1966]

**41. Phoridae** (Fig. 39.26E). A very aberrant family of small to minute flies, with a characteristic, hunchbacked appearance. The wings are folded flat over the abdomen at rest, and the legs, particularly the hind femora, are strongly developed. Adults are common and are often seen running with a quick, jerky motion upon foliage or litter. Some have apterous or brachypterous females, which, in at least one species, are transported by the male during copulation. Two species with apterous females and one normal species live as inquiline in termite nests, while another is recorded from ant nests. Larval habits vary greatly. Many are scavengers in carrion and other decomposing organic matter; *Megaselia halterata* is a pest of commercial mushrooms, while *Megaselia scalaris* has been reared from human myiasis, various kinds of micro-carrion, onion bulbs, faeces, milk, boot polish and paint (Robinson 1971). Some species oviposit and develop satisfactorily in bacterial cultures on ordinary agar plates (Riek unpubl.) and can be pests in laboratory cultures. Others are probably endoparasites, while at least one species lives as an ectoparasite attached to the neck of ants of the genus *Camponotus* (Riek unpubl.). [Beyer 1960; Borgmeier 1963, 1966, 1967]

### Superfamily SYRPHOIDEA

This group approaches the Schizophora more closely than does any other of the Aschiza. They differ from Schizophora in the absence of a ptilinal fissure (but see p. 731), and from all but a few of that group in the very long cell CuP. Though very variable, the larvae are basically of the 'musoid' type.

**42. Pipunculidae** (Dorilidae; Figs 39.27C, D). Rather small flies with remarkable powers of hovering in confined spaces. The larvae are endoparasites of auchenorrhynchous Hemiptera. The commonest genus is *Pipunculus* (= *Dorilas*), with pigmented pterostigma and venation complete except for the absence of  $M_2$ . *Tomosvaryella* is similar, but without pterostigma, whereas *Cephalops* and *Eudorylas* have  $M_{1+2}$  forked (identification of the last two genera is provisional). *Beckerias* with vein 1A obsolescent, and *Chalarus* with discal cell and

$M_1$  also incomplete, occur in eastern Australia. [D. E. Hardy 1964]

**43. Syrphidae** (hover flies; Figs 39.27A, B). A common, widespread family of flies, many with characteristic yellow markings on the body. Some are stoutly built, closely resembling bees or muscoid flies; others (e.g. *Ceriana*, *Allobaccha*) are quite remarkable wasp-mimics, with waisted abdomen and appropriate markings (Plate 6, U; Fig. 3.32). *Psilota rubra* even flies in association with the bee that it mimics.

The adults are swift fliers, and many species habitually hover, apparently motionless, in the air; hence their vernacular name of 'hover fly'. In warm, sunny weather, they are a common sight, either on the wing or visiting blossom, and they are important pollinators of plants. Certain larvae (Syrphinae) are also beneficial, being important predators of aphids, but a few species of *Eumerus* are injurious to plant bulbs. Most larvae are maggot-like in appearance, living in rotting vegetation or fruit, or in liquid media; among the last are the 'rat-tailed maggots' of *Eristalis* spp., which are common in drains. The extraordinary larvae of *Microdon* spp. (Fig. 39.11D) are oval and convex dorsally, soft and flat ventrally, and were originally described as molluscs! They are found in ant nests, where the larvae live as scavengers or predators.

In Australia, the family seems to be rather poor in species, and may be a relatively recent element of the fauna. Quite a few of our species (some 25, in 9 genera) also occur in other countries. Some are obviously recent immigrants (e.g. the cosmopolitan 'drone fly', *Eristalis tenax*), but others belong to wide-ranging species, or perhaps species-complexes, principally Oriental in distribution. The dominant genera in Australia are *Ceriana*, *Microdon*, *Melangyna*, *Simosyrphus*, *Eristalis* and *Psilota*, the last being poorly represented in other countries but relatively abundant here. [G. H. Hardy 1933a; Paramonov 1955a, c, 1956, 1957a; Vockeroth 1969]

### Series Schizophora

A clearly demarcated group, including the most recently evolved families of Diptera, some of them probably still actively radiating; characterised by the presence of the ptilinal fissure and the venation (Fig. 39.7c) which is rather uniform throughout the group.

### Key to the Families of Schizophora Known in Australasia

1. Coxae of each pair little or not separated (except Braulidae with mesonotum short, resembling abdominal tergites); in adult stage not parasitic on vertebrates ..... 2
- Coxae of both mid and hind legs widely separated; mesonotum large, thorax depressed; parasitic on mammals and birds ..... 69
- 2(1). Proboscis vestigial; subcranial cavity much reduced (Fig. 39.38B) ..... 3
- Proboscis developed; subcranial cavity not much reduced ..... 6
- 3(2).  $R_1$  setulose above; ♂ abdomen with  $S_6$  large, symmetrical; ♀ arista with several plumose branches ..... Ctenostylidae
- $R_1$  without setulae; ♂  $S_6$  vestigial or laterally placed; arista not as above ..... 4
- 4(3). Prosternum greatly swollen and prominent, bristled laterally ..... Tachinidae (pt, p. 783)
- Prosternum not prominent ..... 5
- 5(4).  $M_{1+2}$  almost straight, ending in wing margin; lower calypter vestigial (Fig. 39.36E) ..... Gasterophilidae (p. 784)
- $M_{1+2}$  curved forwards to meet  $R_5$ ; lower calypter large ..... Oestridae (p. 784)
- 6(2). One or more strong vibrissae usually present; incurved lower fronto-orbital bristles usually present; Sc more or less

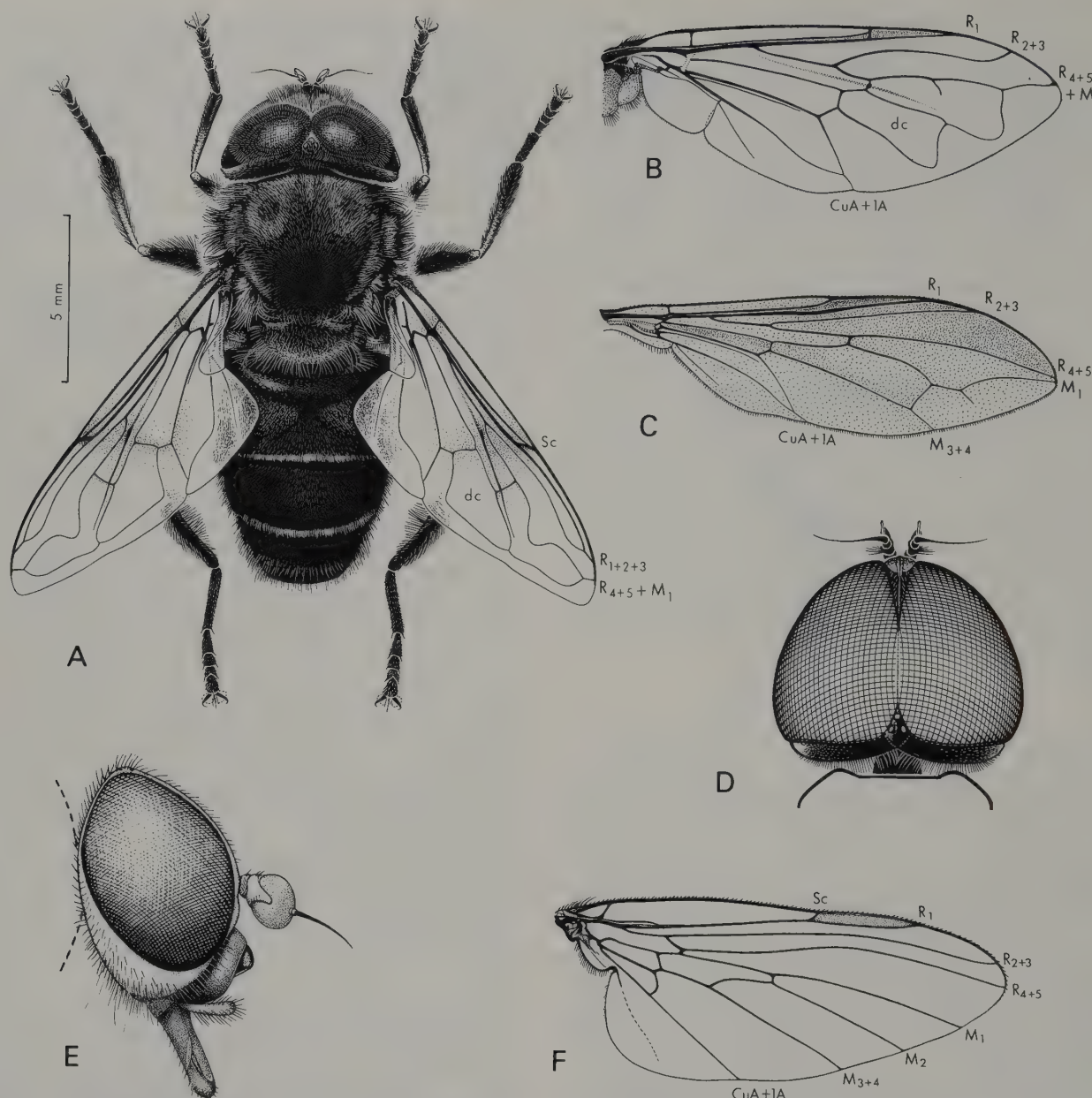


Fig. 39.27 Syrphoidea: A, *Eristalis tenax*, Syrphidae; B, *Microdon fergusonii*, Syrphidae; C, *?Eudorylas* sp., Pipunculidae, wing; D, same, ♂ head, dorsal view; E, *Ironomyia nigromaculata*, Ironomyiidae, head, lateral view; F, same, wing. [A–D by T. Binder; E, F by B. Rankin]

- complete and separate from  $R_1$ ; lower calypter usually well developed (except in some Anthomyiidae and Fanniidae);  $R_1$  without a continuous series of dorsal setulae from near *hm* to apex; transverse sulcus of mesoscutum complete ..... (calyptate families) 63
- Not as above; if vibrissae and incurved lower fronto-orbitals both present, then *Sc* incomplete; lower calypter vestigial, except in many Platystomatidae, which have a continuous series of dorsal setulae on  $R_1$  from near *hm* to apex; transverse sulcus of mesoscutum usually broadly interrupted medially ..... (acalyptate families)\* 7
- 7(6). Wings absent; mesoscutum short, resembling abdominal tergites; scutellum absent ..... **Braulidae** (p. 780)
- Wings usually present; mesoscutum large; scutellum present ..... 8
- 8(7). *Sc* complete, separate from  $R_1$  throughout or joined to it only by a cross-vein ..... 9
- Sc* either indistinct distally, or not ending in costa independently of  $R_1$ , or joined to  $R_1$  by sclerotisation of the intervening region ..... 30
- 9(8). Tarsi with terminal segment triangular, wider than other segments, its distal margin with 2 or 3 setiferous teeth

\* Some aberrant specimens, family 92 (p. 782) will come out here. They are recognisable by the bizarre male antennae, with segment 3 enlarged and divided into 2 or 3 porrect lobes (Fig. 39.38D).



- above claws; antenna decumbent, with segment 3 spheroidal (Figs 39.30C, D) ..... **Coelopidae** (p. 768)
- Terminal tarsal segment not as above; antenna variable, usually either porrect or with segment 3 oval ..... 10
- 10(9). Metathoracic spiracle with one or more fine bristles on lower margin; face with a row of bristles on each side, from which the vibrissae are usually not well differentiated; palps vestigial; ant-like flies with abdomen constricted basally (Fig. 39.29F) ..... **Sepsidae** (p. 769)
- Lower margin of metathoracic spiracle without fine bristles; other characters not all as above ..... 11
- 11(10). One or rarely 2 pairs of outstanding vibrissae present; costa broken or weakened at end of Sc ..... 12
- Vibrissae absent, or vibrissal angle with a row of undifferentiated setulae (except in a few *Lauxaniidae* with unbroken costa) ..... 14
- 12(11). Second antennal segment with angular projection near middle of outer side of distal margin; postvertical bristles, when present, divergent; face largely desclerotised and continuous with lining of subcranial cavity below (Fig. 39.31A) ..... **Clusiidae** (p. 774)
- Second antennal segment without angular projection on outer side; postvertical bristles, when present, convergent; face usually evenly sclerotised with well defined lower margin ..... 13
- 13(12). ☒ Wing membrane with large bare zone; 2 strong mesopleural bristles present; arista plumose (bipectinate) (Figs 39.34F, G) ..... **Curtonotidae** (p. 777)
- Wing membrane almost uniformly microtrichiose; mesopleural bristle rarely present, if present arista not plumose (Figs 39.30A, B) ..... **Heleomyzidae** (pt, p. 771)
- 14(11). Tibiae with preapical dorsal bristles; costa unbroken ..... 15
- Tibiae without preapical dorsal bristles; or if these present, costa broken at end of Sc ..... 19
- 15(14). CuA+1A discontinued well before margin ..... 16
- CuA+1A discernible approximately to margin ..... 17
- 16(15). S1 well developed, sclerotised; anepisternite with one or 2 mesopleural bristles; fronto-orbital bristles 1 or 2; vein 2A generally visible beyond alula (Figs 39.30G, H) ..... **Lauxaniidae** (p. 770)
- S1 vestigial; either anepisternite without strong bristle, or fronto-orbitals 3; vein 2A not visible beyond alula (New Zealand) ..... **Huttoninidae**
- 17(15). ☒ Prothorax with well developed precoxal bridges; sea-shore insects ..... **Helcomyzidae**
- Prothorax without precoxal bridges; insects rarely inhabiting sea-shore ..... 18
- 18(17). ☒ Costa with spaced anterior spines (Fig. 39.29E); prelabrum narrowly separated from face, anteriorly protruding; 2 strong sternopleural bristles present; antennal segment 2 short ..... **Helosciomyzidae** (p. 768)
- Costa without spaced spines; prelabrum distant from face, inconspicuous; either sternopleural bristles vestigial, or antennal segment 2 elongate, cylindrical ..... **Sciomyzidae** (p. 768)
- 19(14). The 2 scutellar bristles arising from apices of long processes; cell M and discal cell broadly confluent. (Eyes and antennae generally borne on lateral processes of head in both sexes) ..... **Diopsidae**
- Scutellar bristles not at apices of long processes (except in a few *Platystomatidae*); cell M nearly always closed ..... 20
- 20(19). Either free section of CuA indented so that cell CuP is produced into an acute lobe (Fig. 39.28G) or R<sub>1</sub> setulose above ..... 21
- CuA not thus indented; R<sub>1</sub> bare ..... 24
- 21(20). Vein R<sub>1</sub> bare, or (rarely) setulose on distal half only ..... **Otitidae** (p. 770)
- Vein R<sub>1</sub> setulose above, at least from just beyond *hm* to apex ..... 22
- 22(21, 30). Incurved lower fronto-orbital bristles present; costa broken at end of Sc; ocelli present; S1 and S2 separate (Figs 39.8C, 28G) ..... **Tephritidae** (p. 771)
- Incurved lower fronto-orbital bristles absent; other characters variable ..... 23
- 23(22). S1 and S2 usually fused (line of demarcation often visible); cell CuP usually acutely produced, with vein CuA indented; ocelli often reduced or absent; in ♀ abdominal segment 6 similar to but shorter than segment 5 (Fig. 39.28F) ..... **Pyrgotidae** (p. 770)
- With none of the above characters; in ♀ T6 and S6 of segment 6 much reduced, usually concealed (Figs 39.28C, D) ..... **Platystomatidae** (p. 770)
- 24(20). ☒ Mid-coxal prong absent; proboscis usually slender, often much longer than head (if proboscis short, then veins R<sub>4+5</sub> and M<sub>1+2</sub> fused apically, and antenna with very short terminal style instead of arista); palp small or absent; cell CuP acute distally, usually long (except *Stylogaster*) (Figs 39.28A, B) ..... **Conopidae** (p. 768)
- Mid-coxal prong present; proboscis never very elongate; arista elongate; palp rarely reduced; cell CuP usually short ..... 25
- 25(24). Prothorax with broad precoxal bridges; hind femur enlarged, with double row of ventral spines (*Gobrya*) ..... **Nothybidae**
- Prothorax without precoxal bridges; hind femur at most slightly larger than mid femur ..... 26
- 26(25). Body elongate; legs, except sometimes the fore pair, very long and slender ..... 27
- Body somewhat compact; legs not remarkably elongate ..... 28
- 27(26). Arista dorsal; mid tibia without apical ventral spur (Fig. 39.29A) ..... **Micropezidae** (p. 771)
- Arista terminal or almost so; mid tibia with strong apical ventral spur (Fig. 39.29B) ..... **Neriidae** (p. 771)
- 28(26). Anepisternite with posterior marginal and upper anterior bristles ..... **Lonchaeidae** (p. 770)
- Anepisternite bare ..... 29

- 29(28). Costa broken at end of Sc; wing usually with apical spot; body colour brown or fulvous (*Neomaorina*) ..... Pallopteridae  
Costa unbroken; wing generally unmarked; body colour otherwise (Fig. 39.30F) ..... **Chamaemyiidae** (p. 769)
- 30(8). R<sub>1</sub> with a series of setulae above; abdominal segment 7 of ♀ forming an ovipositor sheath, not completely retractile ..... 22  
R<sub>1</sub> not setulose; segment 7 of ♀ variable ..... 31
- 31(30). Lower fronto-orbital bristles incurved, upper ones otherwise directed ..... 32  
Incurved lower fronto-orbitals absent ..... 40
- 32(31). Costa broken just beyond *hm*, and also at end of Sc vestige ..... 33  
Costa not broken near *hm* ..... 36
- 33(32). Anepisternite with dorsally directed upper bristle; face with 2 quite separate deeply concave sclerotised plates (New Zealand, etc.) ..... Carnidae-Carninae  
Anepisternite without such bristle; sclerotised part of face undivided, though sometimes biconcave ..... 34
- 34(33). Cells M, CuP and discal open; marginal fringe of alula very long (Fig. 39.32E) ..... **Xenasteiidae** (p. 775)  
Cell M small but enclosed; cells CuP and discal usually enclosed; marginal fringe on alula not much longer than on rest of wing ..... 35
- 35(34). CuA + 1A absent; either proboscis elongate with slender labella, or distal costal break deeply incised, entering costal cell (Figs 39.35A, B) ..... **Milichiidae** (pt, p. 779)  
CuA + 1A extending well beyond cell CuP; proboscis rather short with short broad labella; distal costal break not thus incised (Figs 39.32C, D) ..... **Carnidae-AUSTRALIMYZINAE** (p. 775)
- 36(32). Arista long-plumose (bipectinate); cell CuP absent or open distally ..... 37  
Arista not plumose, usually short-haired; cell CuP usually closed ..... 38
- 37(36). Radial sector towards base with 2 or 3 long dorsal bristles; mesoscutum with general covering of hairs and no differentiated acrostichals (*Neurochaeta*) (Figs 39.33E, F) ..... **Neurochaetidae** (pt, p. 777)  
Radial sector without bristles; mesoscutum with single median series of setulae or bristles, bare between this and dorsocentral series (*Stenomicro*, pt) ..... **Periscelididae** (pt, p. 777)
- 38(36). Postvertical bristles strongly convergent ..... **Chyromyidae-CHYROMYINAE** (pt, p. 772)  
Postvertical bristles divergent ..... 39
- 39(38). Mesopleural bristle present; tibiae without preapical dorsal bristles; ♀ with abdominal segment 7 enlarged, entirely sclerotised (Fig. 39.32A) ..... **Agromyzidae** (p. 775)  
Mesopleural bristle absent; fore and hind tibiae with short preapical dorsal bristles; segment 7 of ♀ not specially developed ..... **Odiniidae** (p. 775)
- 40(31). Hind basitarsus much swollen, or shortened and compressed; vibrissae distinct; fore leg not raptorial; tarsal claws normal (Figs 39.31B, F) ..... **Sphaeroceridae** (p. 772)  
Hind basitarsus similar to fore basitarsus (except in a few Ephydriidae with mantid-like fore legs, and Neurochaetidae with vestigial tarsal claws) ..... 41
- 41(40). Face convex or protuberant, entirely sclerotised; cell CuP incomplete; cell M confluent with discal cell; arista often with long hairs above but at most pubescent below; antennal segment 3 without stiff bristles; post-vertical bristles divergent or absent (Figs 39.34A, B) ..... **Ephydriidae** (p. 777)  
Not as above; if face convex or protuberant, then cell CuP closed, or postvertical bristles convergent, or arista bipectinate, or antennal segment 3 with a series of stiff bristles ..... 42
- 42(41). Cell CuP and vein CuA + 1A absent; cell M confluent with discal cell ..... 43  
Cell CuP at least partly enclosed, or vein CuA + 1A distinct in part ..... 45
- 43(42). Costa with break just beyond humeral cross-vein in addition to that at end of Sc vestige; anepisternite bristled dorsally and posteriorly; face sclerotised except on a linear median strip ..... Chyromyidae-Nannodastiinae  
Costa entire, or broken only at end of Sc; mesopleural bristles absent; face not as above ..... 44
- 44(43). Propleuron with lateral part flat and separated from transverse anterior part by a vertical carina; M<sub>1</sub> usually at least slightly bent at junction with cross-vein *im*, and not notably converging with R<sub>5</sub> towards apex; costa usually broken just before end of R<sub>1</sub> (Fig. 39.35G) ..... **Chloropidae** (p. 780)  
Propleuron sloping inwards anteriorly, without vertical carina; M<sub>1</sub> not at all bent at junction with *im* (which may be absent), thereafter curving forward to converge with R<sub>1</sub>; costa unbroken (Fig. 39.33J) ..... **Asteiidae** (p. 777)
- 45(42). Antennae (except for arista) short, lying in deep pits level with lower margin of eye; ptilinal fissure highly arched, reaching well above antennae; fronto-orbital bristles, when present, directed outwards; postvertical bristles divergent or parallel; costa unbroken (Fig. 39.32B) ..... **Fergusoninidae** (p. 775)  
Antennae and ptilinal fissure not as above ..... 46
- 46(45). M<sub>4</sub> absent beyond discal cell; 1 outwardly directed and 2 proclinate fronto-orbital bristles present; postverticals strong, divergent; mesopleural and sterno-pleural bristles absent (Fig. 39.28E) ..... **Cypselosomatidae** (p. 771)  
M<sub>4</sub> at least faintly discernible beyond discal cell; without the above combination of bristle characters ..... 47
- 47(46). Four or 5 dorsocentral bristles present, at least 1 in front of suture; postvertical bristles convergent or parallel; anepisternite bristled; CuA + 1A absent beyond cell CuP; habitat sea-shore or estuarine (except *Pelomyia* with only 1 fronto-orbital) (Figs 39.35E, F) ..... **Tethinidae** (p. 779)  
Either with fewer dorsocentrals, or postverticals divergent, or anepisternite bare, or CuA + 1A developed ..... 48
- 48(47). Mid tibia with distinct preapical dorsal bristles; all fronto-orbital bristles reclinate, or, if 1 proclinate, then 2 preapi-



	cal dorsal bristles and 1 anterior bristle present on mid tibia; postvertical bristles convergent; prosternum without precoxal bridges (Figs 39.30A, B) .....	<b>Heleomyzidae</b> (pt, p. 771)
	Tibiae without preapical dorsal bristles, except many <i>Drosophilidae</i> which have a proclinate fronto-orbital bristle, only 1 preapical bristle on mid tibia, and prosternum with precoxal bridges .....	49
49(48).	Sc not obsolete apically, either terminating in R <sub>1</sub> or joined to it apically by sclerotisation of intermediate region; postvertical bristles more or less divergent; costa broken at end of Sc only .....	50
	Sc obsolete apically, free from R <sub>1</sub> ; other characters variable .....	51
50(49).	CuA + 1A not distinctly sclerotised beyond cell CuP; 2A often visible; subcranial cavity enlarged (except <i>Zalea</i> with transverse section of CuA indistinct); generally inhabiting sea-shore (Figs 39.35C, D) ...	<b>Canacidae</b> (p. 779)
	CuA + 1A well developed; 2A vestigial; subcranial cavity not enlarged (Fig. 39.31E) .....	<b>Piophilidae</b> (p. 770)
51(49).	Arista of antenna absent, or minute and terminal on the very large antennal segment 3; vertical, ocellar and fronto-orbital bristles not differentiated ( <i>Cryptochetum</i> ) (Fig. 39.34C) .....	<b>Cryptochetidae</b> (pt, p. 778)
	Arista well developed, or, if vestigial, replaced by a long, haired process .....	52
52(51).	Antennal segment 2 cap-like, with linear dorsal slit; arista usually bipectinate .....	53
	Antennal segment 2 not cap-like, without linear slit; arista rarely bipectinate .....	56
53(52).	Costa broken beyond <i>hm</i> as well as at end of Sc; proclinate fronto-orbital generally present; postverticals more or less convergent (Figs 39.34D, E) .....	<b>Drosophilidae</b> (p. 778)
	Costa at most broken only at end of Sc; proclinate fronto-orbital present or absent; postverticals not usually convergent .....	54
54(53).	Distal desclerotised section of Sc transverse, bent almost at right angles to the mainly sclerotised basal part, and ending in the distinct costal break; anepisternite with spaced, socket-based hairs (Fig. 39.31G) .....	<b>Psilidae</b> (p. 770)
	Distal part of subcosta not as above, if somewhat transverse, then costa unbroken; anepisternite bare or pubescent .....	55
55(54).	Tarsal claws vestigial; head much flattened; arista with minute hairs only ( <i>Nothoasteia</i> ) .....	<b>Neurochaetidae</b> (pt, p. 777)
	Tarsal claws normal; head not flattened; arista long-plumose ( <i>Cyamops</i> , <i>Stenomicro</i> (pt), <i>Periscelis</i> ) (Figs 39.33C, D, G, H) .....	<b>Periscelididae</b> (pt, p. 777)
56(52).	Arista long-plumose; antennal segment 3 markedly decumbent; wing narrowed basally with reduced alula .....	<b>Anthomyzidae</b> (p. 777)
	Arista with hairs short and not seriate, or absent; other characters usually not entirely as above .....	57
57(56).	Presutural bristle present .....	58
	Presutural bristle absent .....	61
58(57).	A strong, proclinate fronto-orbital bristle present; costa, at end of Sc, with very deep incision recurrent into costal cell (Figs 30.35A, B) .....	<b>Milichiidae</b> (pt, p. 779)
	Proclinate fronto-orbital absent; costal incision not remarkably deep .....	59
59(58).	One strong fronto-orbital bristle present; cross-veins <i>r-m</i> and <i>im</i> very close together; vein CuA + 1A very long but weak .....	<b>Teratomyzidae</b> (p. 777)
	More than 1 strong fronto-orbital present; the above cross-veins less strongly approximated; vein CuA + 1A usually shorter, but well sclerotised .....	60
60(59).	Scutellum with 2 subequal pairs of bristles; 1 or 2 pairs of dorsocentrals present .....	<b>Chyromyidae-CHYROMYINAE</b> (pt, p. 772)
	Apical pair of scutellar bristles more than twice as long as other scutellars; at least 4 pairs of dorsocentrals present .....	<b>Pseudopomyzidae</b> (p. 771)
61(57).	Mesopleural bristle present; face desclerotised medially; prelabrum enlarged (Fig. 39.29C) ...	<b>Tanypezidae</b> (p. 770)
	Mesopleural bristle absent; face entirely sclerotised; prelabrum rather small .....	62
62(61).	Proclinate fronto-orbital bristle present; post-vertical bristles parallel or divergent; apical pair of scutellar bristles normally erect (Figs 39.33A, B) .....	<b>Aulacigastridae</b> (p. 777)
	Proclinate fronto-orbital bristle absent; postvertical bristles strongly convergent; apical pair of scutellar bristles not erect, normally crossed ( <i>Librella</i> ) .....	<b>Cryptochetidae</b> (pt, p. 778)
63(6).	Hypopleuron (meropleuron) usually bare or with weak hairs; if bristled, then pteropleuron bare and M <sub>1</sub> not distinctly bent forward .....	64
	Hypopleuron (meropleuron) with a row or group of bristles and pteropleuron with one or more bristles, or occasionally either hypopleuron or pteropleuron with long dense hairs only; M <sub>1</sub> almost always strongly bent forward distally .....	67
64(63).	Orbital plates much broader than interfrons, usually contiguous medially, or vertex and frons horizontal, much shorter than head-width; ♂ with antennal segment 3 greatly enlarged, either entire, axe-head like, or deeply dissected to yield 2 or 3 digitate, porrect lobes; ♀ with conspicuous oviscapt, downcurved, dorsoventrally flattened, and truncate at apex (Figs 39.38C, D) .....	family 92 (p. 782)
	Orbital plates and/or antennae, and oviscapt otherwise .....	65
65(64).	CuA + 1A reaching wing margin (sometimes very faint distally); scutellum almost always with tuft of fine hairs beneath apex; lower calypter not longer than upper calypter (Fig. 39.36C) .....	<b>Anthomyiidae</b> (p. 780)
	CuA + 1A not reaching margin; scutellum without such hairs; lower calypter almost always longer than upper	

- calypter ..... 66
- 66(65). Hind tibia with a true dorsal submedian bristle in line with the preapical dorsal bristle; CuA + 1A very short, its imaginary extension meeting that of vein 2A before the wing margin ..... **Fanniidae** (p. 780)
- Hind tibia without such a bristle; CuA + 1A otherwise (Figs 39.36A, B) ..... **Muscidae** (p. 780)
- 67(63). Subscutellum prominent, as a transverse, rounded lobe beneath scutellum and above normal postnotum (rather weak in Palpostomatini, which have the arista bare or pubescent and labella often with a pair of palp-like processes posteriorly); anterior lappet of metathoracic spiracle without tuft of long hairs (Fig. 39.38A) ..... **Tachinidae** (pt, p. 783)
- Postnotum normal, without distinct, rounded subscutellum dorsally; or, if subscutellum distinct (blue or green, metallic species), anterior lappet of metathoracic spiracle with tuft of long, fine hairs towards dorsal margin ..... 68
- 68(67). Colour non-metallic, thorax usually with longitudinal dark stripes; external posthumeral bristle, if present, never distinctly lateral to presutural bristle;  $M_1$  angled at a point usually nearer to apex of discal cell than to wing margin; posterior spiracle not enlarged, set posterior to line of meropleural bristles; if arista bare, base of R without setae posteriorly (Fig. 39.37A) ..... **Sarcophagidae** (p. 782)
- Colour metallic; or external posthumeral bristle distinctly lateral to presutural bristle; or  $M_1$  angled at a point nearer to wing margin than to apex of discal cell; or posterior spiracle very large, partly projecting beyond main axis of line of meropleural bristles; if arista bare, base of R with setae posteriorly (Fig. 39.37B) ..... **Calliphoridae** (p. 781)
- 69(1). Head small and inserted dorsally on thorax; wingless; parasites of bats (Fig. 39.39B) ..... **Nycteribiidae** (p. 786)
- Head larger, not inserted dorsally on thorax; usually winged ..... 70
- 70(69). Palps appressed, sheathing the proboscis, not broadened; head usually closely fitted to thorax; when wings present, the stronger veins crowded towards costa; parasites of birds and mammals other than bats (Fig. 39.39A) ..... **Hippoboscidae** (p. 785)
- Palps not appressed and sheathing, extremely broad; head not closely fitted to thorax; veins not crowded towards costa in winged forms; parasites of bats (Fig. 39.39C) ..... **Streblidae** (p. 785)

#### Superfamily CONOPOIDEA

This is possibly a sister group to the rest of the Schizophora. The venation resembles that of the Syrphoidea in having  $M_1$  approximated to or fused with  $R_5$  distally, cell CuP long and acute (except in *Stylogaster*), and often a vestige of the vena spuria present. The male postabdomen is quite symmetrical.

**44. Conopidae** (Figs 39.28A, B). A rather small family, but unusual in that most of its members are wasp-mimics, some very effectively so (Plate 6, Q). Many superficially resemble syrphids of the genus *Ceriana*, even in venation, but all have a well-developed ptilinum. *Stylogaster* has an aberrant venation, but is recognisable by the long, thin proboscis (present in many conopids) and the elongate ovipositor. Most conopids have both male and female terminalia enlarged and conspicuous, those of the female often opposed or covered by a large lobe developed from S5. Adults fly slowly, and are usually seen on blossom, often accompanying the wasps which they mimic; *Stylogaster* often hovers near the ground. Larvae of Australian species presumably resemble those of other countries, which are recorded as endoparasites of adult Hymenoptera, Diptera and orthopteroids (K. G. V. Smith and Cunningham-van Someren 1986). The 16 Australian genera include the widely distributed *Conops*, *Myopa*, *Physocephala*, *Stylogaster* and *Thecophora*; the remainder are mostly endemic, though species of *Microconops* are also found in Chile. [Kröber 1939; Camras 1961; K. G. V. Smith 1979]

#### Superfamily SCIOMYZOIDEA

Incurved fronto-orbital bristles and vibrissae generally absent; antennal segment 2 without dorsal notch or slit;

costa unbroken; Sc complete and distally diverging from  $R_1$ ;  $R_1$  usually without macrotrichia; cell CuP short, not angularly produced; vestige of 2A usually visible beyond alula. Protandrium with S6 and S7 laterally displaced, or symmetrical through reduction. Female postabdomen with segment 7 not modified to form an ovipositor sheath, the cerci generally separate.

This superfamily may be paraphyletic as most of its characters are probably plesiomorphic for the Schizophora. The Lauxanioidea are sometimes separated from the Sciomyzoidea, but neither degree of reduction of CuA+ $A_1$  nor degree of protandrial symmetry provides a quite satisfactory basis for this division. The Huttoniidae (New Zealand), Dryomyzidae (mainly Holarctic), Helcomyzidae (temperate zones including New Zealand), Ropalomeridae and Eurychoromyiidae (Neotropical) have not been found in Australia.

**45. Sciomyzidae** (Tetanoceridae; Fig. 39.29D). The larvae are predators or parasitoids of freshwater and terrestrial snails. Free-living larvae and floating puparia of *Dichetophora* are common in ponds and dams. These and larvae of *Sepedon* are important predators of snails that may carry liver-fluke. The adult of *Sepedon* is remarkable for the absence of the ptilinal fissure.

**46. Helosciomyzidae** (Fig. 39.29E). The known larvae appear to be fungivorous (Steyskal and Knutson 1978), saprophagous or predatory on insects (possibly mainly ant larvae, Barnes 1980). The family includes *Helosciomyza* (Australia and New Zealand), *Eurotocus* (Australia), *Xenosciomyza* and *Polytocus* (New Zealand) and *Sciogriphoneura* (Chile). [Steyskal and Knutson 1978]

**47. Coelopidae** (Figs 39.30D, E). Adults are adapted to



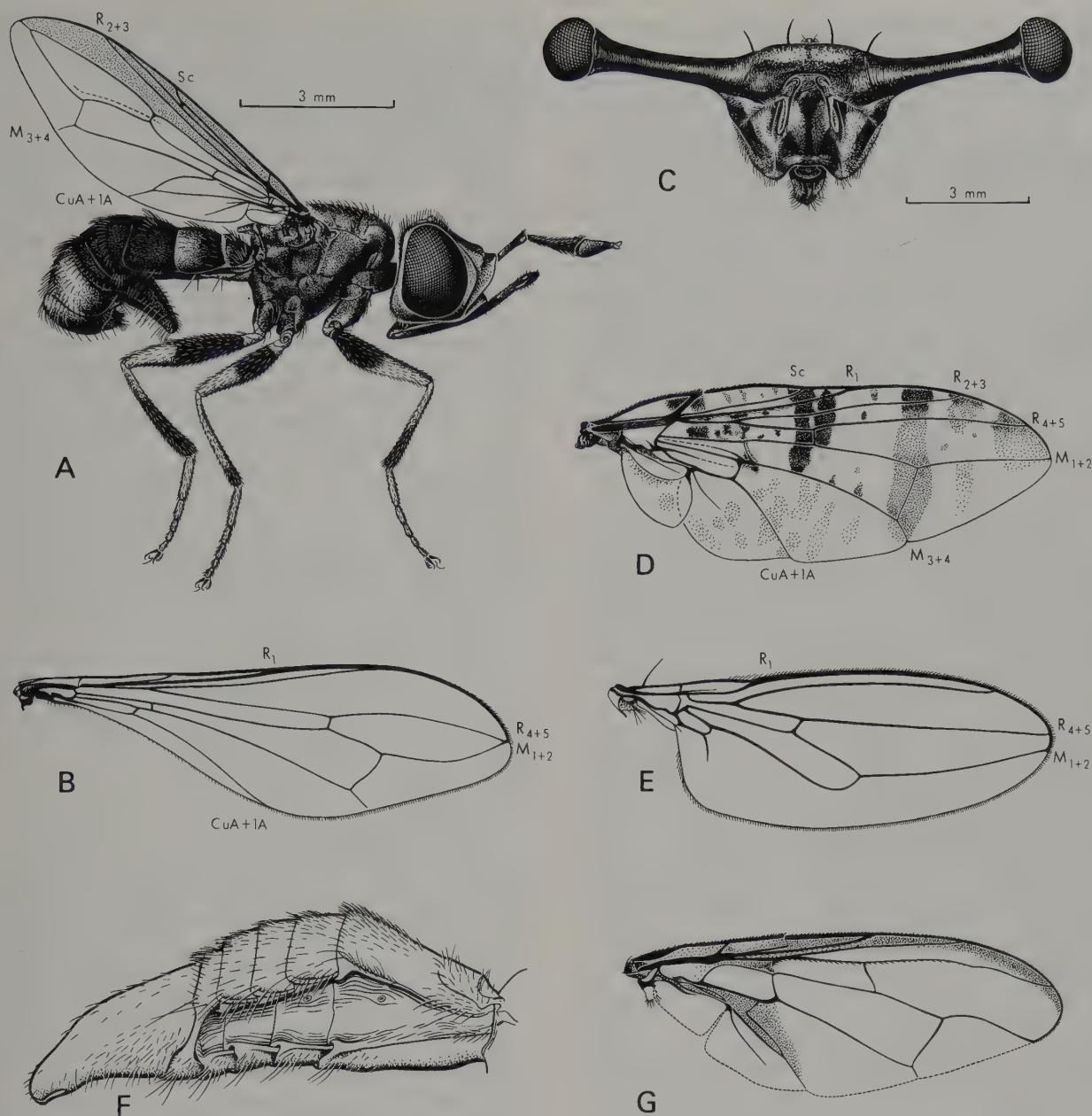


Fig. 39.28 A, *Conops splendidus*, Conopidae, ♀; B, *Stylogaster* sp., Conopidae; C, *Achias australis*, Platystomatidae, ♂, frontal view of head; D, *Euprosopia tenuicornis*, Platystomatidae; E, *Cypselosoma australe*, Cypselosomatidae; F, *Adapsilia illingworthana*, Pyrgotidae, abdomen; G, *Dacus tryoni*, Tephritidae. [T. Binder]

living among wet seaweed and on windswept shores. The occiput is usually flattened so that the head fits closely to the thorax, and the cuticle of at least some coelopids is unwettable. The larvae live in stranded kelp and sea grass. The majority of world species occur on Australasian shores, south to Macquarie I. (only 2 Australian species described); but the family is unknown from South America. [Dobson 1976]

**48. Sepsidae** (Fig. 39.29F). Small, ant-like flies with the habit of continuously waving the wings when at rest. Seven genera occur in Australia, but almost all our species occur in, and probably came from, the Oriental Region or Melanesia. The larvae live mainly in mammal

faeces and the adults often swarm nearby, or near mammal carcasses. *Parapalaeosepsis plebeia* also swarms around rotting fruit and compost pits. [Zuska and Colless 1984]

**49. Chamaemyiidae** (Ochthiphiidae, Cremifaniidae; Fig. 39.30F). Small flies; postvertical bristles convergent or absent; at most 2 fronto-orbital bristles present, both reclinate; vein CuA+1A much abbreviated; vein 2A visible beyond alula. The larvae are predators of coccids and psyllids. The genera *Pseudoleucopis*, *Chaetoleucopis*, *Chamaemyia* and *Leucopis* occur in Australia, the first two being endemic. In *Gayomyia*, from Australia and Chile, CuA+1A is long and curved and the protandrium

very asymmetrical; its family position is doubtful. [Malloch 1930; J. F. McAlpine 1960]

**50. Lauxaniidae** (Sapromyzidae; Celyphidae; Figs 39.30G, H). This is one of the largest and commonest of the 'acalyprate' families, the adults occurring in a wide range of habitats: mangrove swamps, sand dunes, grasslands, all forest types, and on the summits of such mountains as Kosciusko and Wellington. R. M. Miller (1977) has listed rearing records of Lauxaniidae, showing that most larvae live in fallen leaves or other rotting vegetation. *Sapromyza flavimana* has been reared from the nest of the scrub tit (*Acanthornis magnus*) in Tas. The adults of many exotic species are known to feed by grazing on fungi on vegetation (Broadhead 1984), and no doubt the same is true in Australia. Malloch has given a key to the Australian genera, but there remain many unrecorded genera and species. [Malloch 1927, 1928; Stuckenberg 1971]

### Superfamily DIOPSOIDEA (Nothyboidea)

Generally elongate flies. Vibrissae absent; postverticals, when present, divergent. Prosternum with broad precoxal bridges (except Psilidae, which may not belong here). Male postabdomen with well-developed segment 6, the sternite ventrally placed. Female usually with terminal segments elongate, but no distinct ovipositor sheath or piercing organ, though cerci may be fused. The Nothybidae (Oriental, but possibly including *Gobrya*, which reaches New Guinea), Syringogastridae (Neotropical) and Diopsidae (= Centrioncidae, which reach New Guinea) do not occur in Australia.

**51. Tanypezidae** (Strongylophthalmyiidae; Fig. 39.29c). Costa broken near end of  $R_1$ ; postvertical bristles divergent; mesopleural bristle present; face desclerotised medially; male with protandrial sternites asymmetrical and without articulated surstyli. The genus *Strongylophthalmyia* is principally Oriental, with 3 undetermined Australian species occurring mainly in rainforest. The male of the commonest Australian species has the arista reduced and replaced by an outgrowth of segment 3 (Fig. 39.29c). The genus, which differs from typical tanypezids in its incomplete Sc, has also been included in the Psilidae or placed in a separate family.

**52. Psilidae** (Fig. 39.31G). Costa broken well before end of  $R_1$ , Sc discontinued opposite the break; face sclerotised; pleural bristles absent; prosternum without precoxal bridges; male postabdomen symmetrical, with or without surstyli. The genus *Chyliza* occurs from North Qld to Vic.

### Superfamily TEPHRITOIDEA (Otitoidea)

Vein  $R_1$  often setulose, cell CuP often acutely produced. Male usually with abdominal segment 6 vestigial or absent, the aedeagus usually very long and coiled. Female with abdominal segment 7 more or less enlarged to form an ovipositor sheath, the subsequent segments forming a retractile tube, terminating in a piercer formed from the fused cerci and T9. The Richardiidae (Neotropical) and Tachiniscidae (Neotropical, Ethiopian) have not been found in Australia. The Ctenostylidae (= Lochmo-

styliinae, formerly included in Pyrgotidae) doubtfully belong here (circumtropical including Indonesia). The classification of the superfamily has been discussed by Steyskal (1961) and J. F. McAlpine (1977).

**53. Lonchaeidae** (Figs 39.31C, D). Stout dark flies of moderate to small size, without wing markings; postfrons of male narrowed. Australia has species of *Lamprolonchaea*, *Lonchaea*, *Dasiops* and *Silba*. The larvae of *Lamprolonchaea brouniana*, the metallic-green tomato fly, often live in damaged tomatoes but are also common in cow dung. [Malloch 1928; J. F. McAlpine 1964]

**54. Piophilidae** (Thyreophoridae; Fig. 39.31E). Postvertical bristles well developed; at most 2 weak fronto-orbital bristles; vibrissae strong; mesopleural bristle absent. The larvae of most species live in dead animal matter. Those of the introduced *Piophila casei* ('cheese skippers') live in cheese, preserved meats, and old carrion. *Piophila australis*, differing in having 4 instead of 2 pairs of dorsocentral bristles, is apparently endemic to Australasia. *Piophilosoma* (= *Chaetopiophila*), an endemic genus, has been placed in the Thyreophoridae, a group not deserving family rank; its larvae live in dried carrion. [D. K. McAlpine 1989]

**55. Otitidae** (Ortaliidae in part, Ulidiidae). Male with aedeagal apodeme simple; female with abdominal segment 6 generally well developed. The Australian species belong to the subfamily ULIDIINAE, having vein  $R_1$  bare and aedeagus not setulose. *Physiphora aenea* is a common introduced species, with metallic, green-black body colour. Its larvae live in decaying vegetable refuse. [Daniels 1976a]

**56. Platystomatidae** (Figs 39.28c, D). Abdominal segment 6 of female vestigial; costa usually broken beyond humeral vein, but not at end of Sc. In this and the next two families, the aedeagal apodeme ('fultella') has a pair of lateral arms which pivot on S9. Adults in many cases feed at fresh mammalian faeces. Larval habits are varied, some living in plant trunks damaged by other insects, or fungi, or in coleopterous tunnels in fallen logs. At least some *Rivellia* larvae live in bacterial root nodules on leguminous plants. Larvae of *Elassogaster linearis* have been found consuming the eggs of *Locusta migratoria*. In Australia, the dominant genera are *Rivellia*, *Duomyia*, *Euprosopia* and *Lamprogaster*. The almost cosmopolitan *Rivellia* includes small species, usually black and with transverse bands on the wings. They occur in most forested parts of Australia, but few have yet been described. *Duomyia* (approx. 88 spp.) is exclusively Australian, with species widely distributed through the continent in open country. *Achias*, *Lamprogaster* and *Euprosopia* are found mainly in wet tropical and subtropical areas, though the last two are represented in the highlands of south-eastern Australia. *Achias*, with 5 species in North Qld and over 80 in New Guinea, usually has the eyes on stalks or lateral extensions of the head in the males (Fig. 39.28c); these function in territorial fighting (D. K. McAlpine 1979). The females are much less modified. [D. K. McAlpine 1973a]

**57. Pyrgotidae** (Fig. 39.28F). Distinguished from Tephritidae by the absence of lower fronto-orbital bristles



and from Platystomatidae in the female by the better developed abdominal segment 6. All but a few pyrgotid species have abdominal S1 and S2 fused (always free in the other 2 families). Other characters, such as absence of ocelli and of the mid-coxal prong, vary in Australian species. As far as known, the larvae are parasites of adult Scarabaeidae, and several Australian species have been observed apparently ovipositing on *Phyllotocus* and *Anoplognathus*. Though the flies are mainly nocturnal, adults of some species also visit flowers in the daytime. [D. K. McAlpine 1978a]

**58. Tephritidae** (Trypetidae, Trypaneidae, Trupaneidae; fruit flies; Figs 39.8C, 28G). Sc usually bent forward distally towards the costa almost at a right-angle; abdominal segment 6 of female usually well developed. A large, cosmopolitan family, best represented in the tropics.

The numerous species of *Dacus* (with several subgenera, sometimes called genera) are fruit-eating in the larval stage. The Qld fruit fly, *Dacus (Bactrocera) tryoni*, is by far the most serious pest species in eastern Australia, attacking a wide range of cultivated and native fruits. Other destructive species in Qld are *Dacus (Austrodacus) cucumis*, principally in cucumbers and other cucurbits, and *Dacus (Afrodacus) jarvisi* in a variety of fruits. *Dirioxa pornia*, of N.S.W. and Qld, is of little importance because it usually attacks damaged fruit. The larvae of *Termitorixa termitoxena*, in the N.T., live in termite galleries in tree trunks, and those of *Phytalmia mouldsi* in fallen logs. The Mediterranean fruit fly, *Ceratitis capitata*, an introduced species, attacks oranges and a wide variety of other cultivated fruits; once a serious pest in N.S.W., it has not been seen there since 1941, but is still of importance in W.A. *Procecidochares utilis* is a Mexican species, introduced into Qld and N.S.W. to control the weed *Eupatorium adenophorum*; eggs are laid in the young shoots which subsequently become galled by the larvae. The Bathurst burr seed fly, *Euaresia bullans*, which is common in N.S.W., also occurs in North and South America, and Europe. Its larvae eat the seeds of the burr (*Xanthium spinosum*) and probably of other plants. The larvae of *Tephritis*, *Trupanea* and *Dioxya* live in the flower-heads of Asteraceae. Species of *Oedaspoides* seem to be associated with Goodeniaceae. [Malloch 1939; Drew 1989; Drew *et al.* 1978]

### Superfamily NERIOIDEA

Legs often very elongate. Prosternum with a strongly sclerotised posterior part which is broadly continuous with mesosternal region; often also with a median anterior plate; precoxal bridges absent. Preapical tibial bristles absent. Male postabdomen with ventral and often almost symmetrical S6, S7 ventral or sublateral. Epandrium often elongate, channelled ventrally to receive the basiphallus which is elongate, rigid, usually with longitudinal struts, the distiphallus usually folded along its anterior side. Female abdomen with segment 7 elongate, forming an ovipositor sheath, the more distal segments telescopic, not forming a piercing organ but with small, separate or incompletely fused cerci. The mainly Oriental Megamerinidae do not occur in Australia.

**59. Pseudopomyzidae**. Medium-sized to minute flies resembling Heleomyzidae in cephalic chaetotaxy, but clearly belonging to this superfamily from the structure of the prosternum and postabdomen of both sexes. The single Australian species of *Pseudopomyza* (= *Heluscolia*) lives in cool damp forests. The family is better represented in New Zealand and especially in the Neotropical Region. [Krivoshchina 1979]

**60. Cypselosomatidae** (Fig. 39.28E). Legs not attenuated; vibrissae and ocellar bristles well developed; 4–6 dorsocentral bristles; mid tibia with strong dorsal bristles; male with almost symmetrical postabdomen, and no pregenital lobes on S5. This small family is represented in Australia by the genera *Cypselosoma* and *Formicosepsis*. The larvae of *C. australe* live in bat guano in caves. The family is known elsewhere only from the Oriental Region and New Guinea. [D. K. McAlpine 1978b]

**61. Neriidae** (Fig. 39.29B). Head elongate, postvertical bristles convergent; 2nd antennal segment with terminal finger-like process on inner side; costa usually without distinct break; CuA+1A not reaching margin; pregenital lobes of male absent; protandrium asymmetrical; segment 9 elongate. The family is widely distributed, but principally tropical. The banana-stalk fly, *Telostylus angusticollis*, occurs in southern Qld and N.S.W. The larvae have been found in the decaying ends of cut banana bunches and in other decaying vegetable matter.

**62. Micropezidae** (Tylidae; Calobatidae; Fig. 39.29A). Ocellar bristles absent or minute; postverticals usually divergent or parallel; 2nd antennal segment without process; costa unbroken; vein CuA straight; male usually with pregenital lobes on abdominal S5, S6 ventral, S7 lateral. The larvae live in decaying wood and other vegetable matter. Two subfamilies occur in Australia: Eurybatinae with 1 or 2 distinct sternopleural bristles and ocelli situated near vertex; and Taeniapterinae with a fascicle of numerous, long sternopleural bristles and ocelli well in front of vertex. The EURYBATINAE include the dominant Australian genus, *Metopochetus*, distinguished by the occipital tubercle just above the neck. It occurs from New Guinea to Tas. and the south-west. *Badisis ambulans*, an apterous, ant-mimicking fly, lives as a larva in the pitchers of *Cephalotus*. The other genera of the subfamily, *Cothornobata* and *Crepidochetus*, are tropical and subtropical only. *Mimegralla* is the only Australian genus of TAENIAPTERINAE. [D. K. McAlpine 1975]

### Superfamily HELEOMYZOIDEA

Postvertical bristles usually convergent; vibrissae usually present; prosternum usually without well sclerotised precoxal bridges; costa weakened or broken at end of Sc; vein 1A not broken where it borders on cell CuP.

**63. Heleomyzidae** (including Trixoscelidae and Rhinotoridae; Figs 39.30A, B). Postvertical bristles convergent (often absent in *Cairnsimyia*); fronto-orbital bristles usually reclinate; sternopleural and usually presutural bristles present; tibiae usually with preapical dorsal bristles; costa weakened or broken at end of Sc; cells CuP and M closed; male postabdomen with S6 and S7 usually laterally displaced or absent. This diverse group is

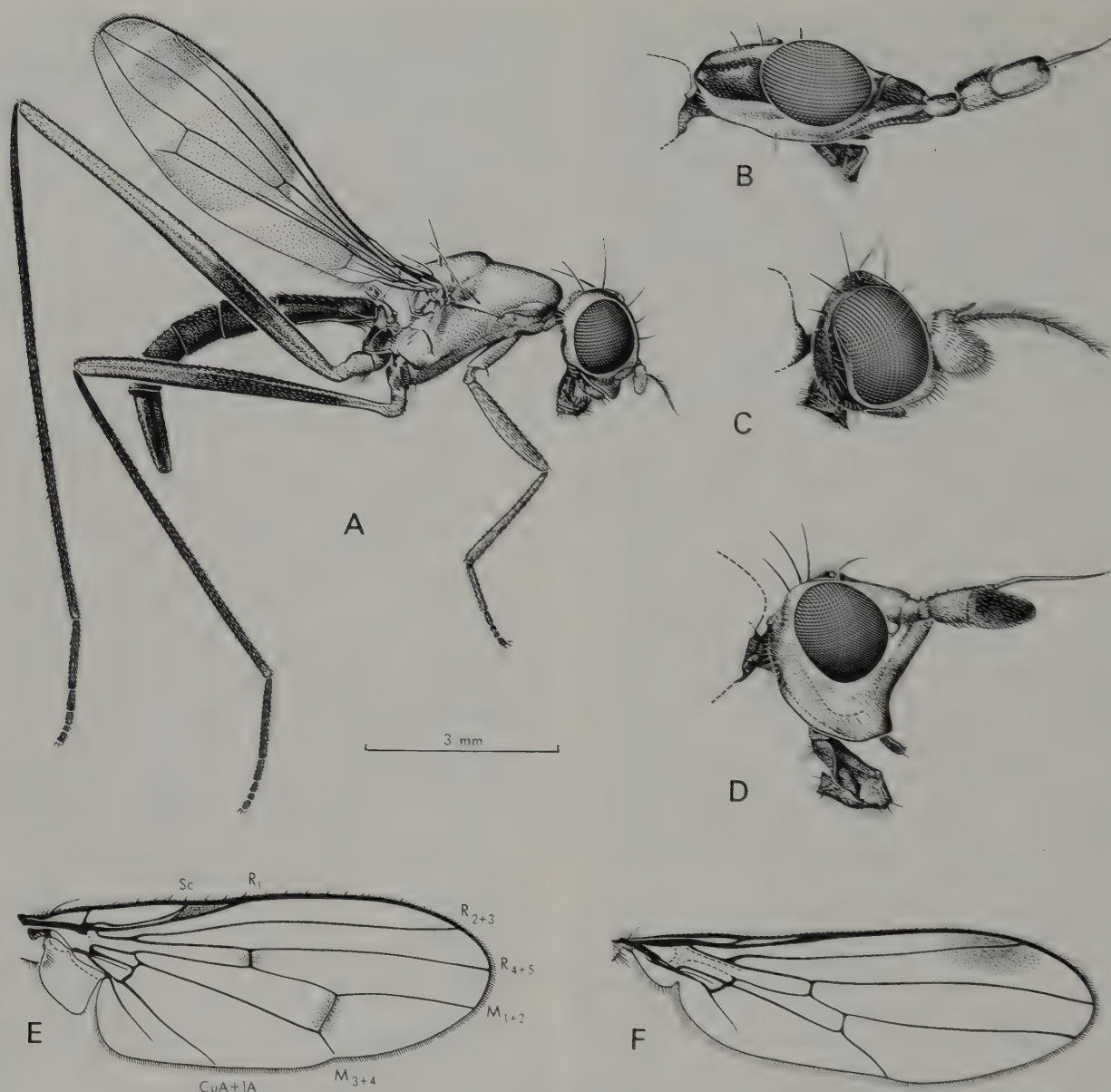


Fig. 39.29 A, *Metopochetus* sp., Micropezidae, ♀; B, *Telostylinus angusticollis*, Neriidae; C, *Strongylophthalmyia* sp., Tanypezidae, ♂; D, *Dichetophora* sp., Sciomyzidae; E, *Helosciomyza* sp., Helosciomyzidae; F, *Australosepsis niveipennis*, Sepsidae.

[T. Binder]

sometimes divided into numerous families (e.g. Griffiths 1972). These flies live mainly in temperate forests. The larvae of *Tapeigaster* live in fructifications of fungi (D. K. McAlpine and Kent 1982), whereas those of *Cairnsimyia* live in borer holes in trees (e.g. *Ficus*, D. K. McAlpine 1968), and those of *Pseudoleria* often live in rat nests.

The principally north-temperate tribe Heleomyzini, with CuA+1A reaching margin and spaced costal spines, is represented by the introduced genera *Pseudoleria* and *Oecothia*. The other Australian genera belong to south-temperate tribes. *Tapeigaster* (tribe Tapeigastriini) includes large, stout flies with no spaced costal spines, 2A visible, and ventrally spined femora (Fig. 39.30A). The largest Australian genus is *Diplogeomyza*, with 4 dorso-

centrals and 2 long preapical dorsal bristles on the mid tibia (tribe Allophylopsini). [D. K. McAlpine 1985a]

**64. Sphaeroceridae** (Borboridae, Cypselidae; Figs 39.31B, F). Small to very minute flies with distinct vibrissae, often found on animal dung or other organic matter in which the larvae live. *Leptocera* (sometimes divided into several genera), with cells M and CuP open, is the dominant genus. *Sphaerocera* and *Copromyza* have these cells closed, the former without, the latter with, major scutellar bristles. *S. curvipes* is an immigrant from Europe. Several brachypterous or apterous species live in leaf litter. [O. W. Richards 1973]

**65. Chyromyidae** (Chiromyiidae). Very small but rather stout, yellow and blackish flies: fronto-orbital bristles reclinate or the foremost somewhat sloping inwards;



vibrissae often not differentiated from cheek bristles; vein Cu+1A not reaching margin. Adults of *Aphaniosoma* and *Gymnochiromyia* (CHYROMYINAE) have been found on flowers (e.g. *Santalum*, *Hibiscus*), and larvae of the latter have been found in bat guano in Australian caves and in nests of British birds.

The very minute Nannodastiinae (Papp 1980), which

occur on Christmas I., in Papua New Guinea, and probably northern Australia, seem better placed in Chyromyidae than in Ephydriidae. They differ from Chyromyinae in the long bristles on the anterior margin of antennal segment 3, in the dorsally displaced posterior notopleural bristle, and in the absence of the postvertical bristle, alula, cell CuP and vein CuA+1A.

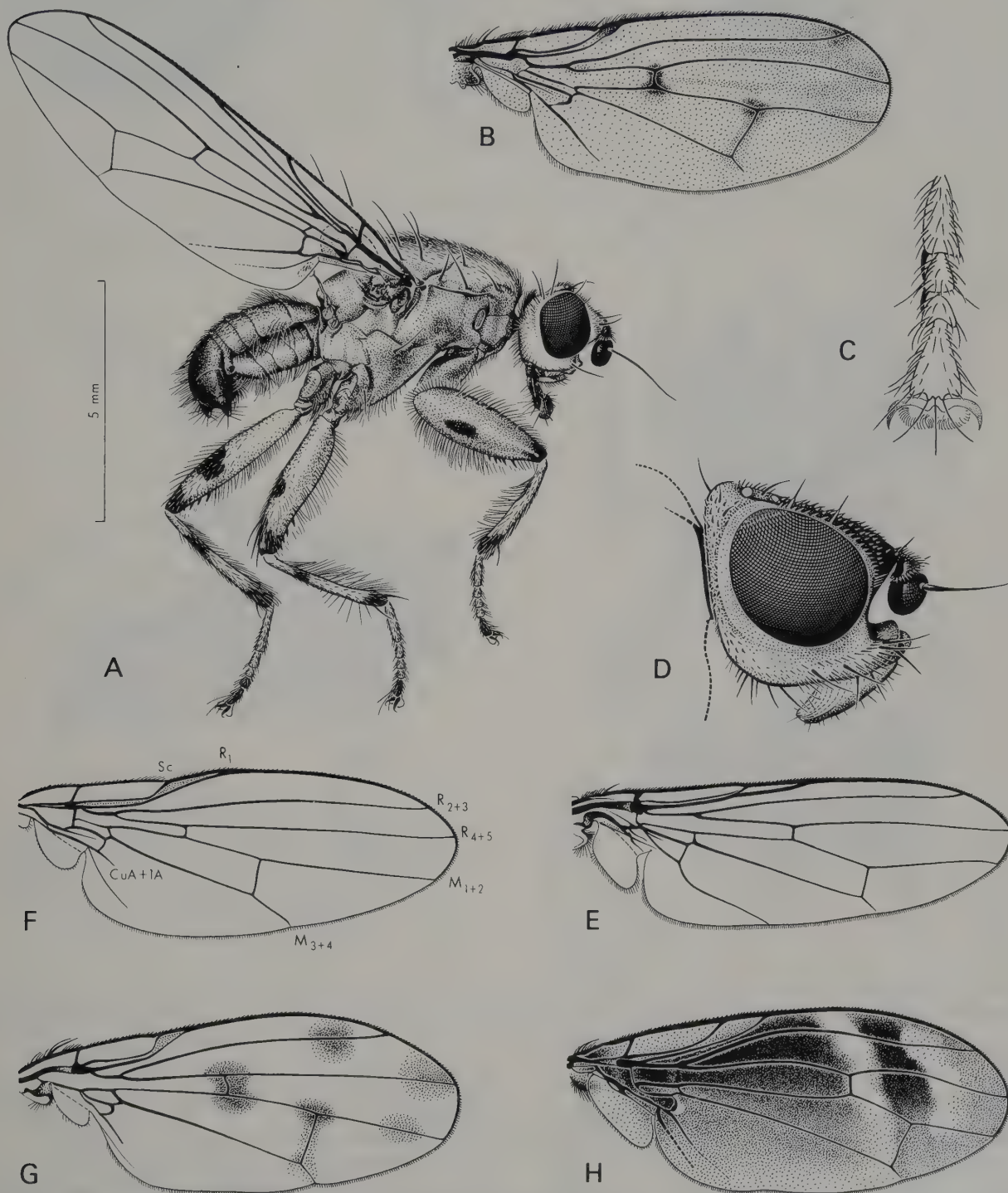


Fig. 39.30 A, *Tapeigaster annulipes*, Heleomyzidae, ♂; B, *Diplogeomyza diaphora*, Heleomyzidae; C, *Chaetocoelopa sydneyensis*, Coelopidae, hind tarsus; D, same, head; E, same, wing; F, *Pseudoleucopis fasciventris*, Chamaemyiidae; G, *Homoneura proximella*, Lauxaniidae; H, *Depressa striatipennis*, Lauxaniidae.  
[T. Binder]

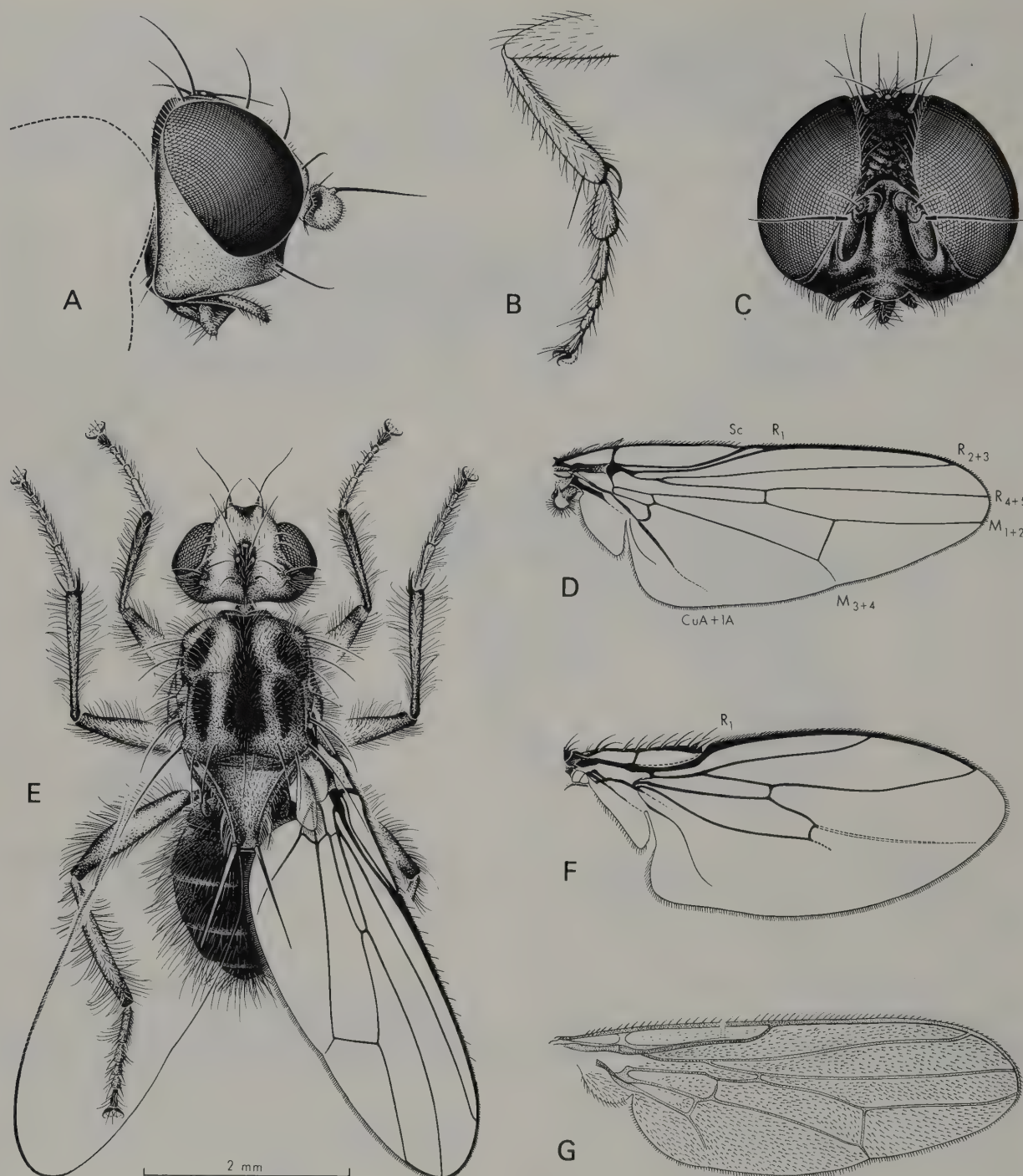


Fig. 39.31 A, *Heteromeringia norrisi*, Clusiidae; B, *Copromyza* sp., Sphaeroceridae, hind leg; C, *Lamprolonchaea brouniana*, Lonchaeidae; D, same, wing; E, *Piophilosoma antipodum*, Piophilidae, ♂; F, *Leptocera* sp., Sphaeroceridae; G, *Chyliza* sp., Psilidae. [A–F by T. Binder; G by S. P. Kim]

### Superfamily OPOMYZOIDEA

Postvertical bristles, when present, generally divergent to parallel; arista never plumose (bipectinate); prosternum usually compact, without precoxal bridges; costa broken at end of Sc (except in Fergusoninidae and Acartophthalmidae); cells M and CuP complete; vein 2A absent; female postabdominal segments elongate, often with fused cerci. Besides the families occurring in Australia,

the Opomyzidae and Acartophthalmidae (Holarctic) belong in the superfamily.

**66. Clusiidae** (Heteroneuridae, Clusioididae; Fig. 39.31A). Second antennal segment with angular projection on outer side; male postabdomen asymmetrical, with T6 and S8 present. Most species are found in wet forest country. The larvae live in moist rotting wood. [D. K. McAlpine 1960]



**67. Odiniidae.** Related to Agromyzidae, but distinguished by the presence of short preapical tibial bristles and the less developed ovipositor. The Australian species are undescribed. One of them apparently oviposits in rotting logs.

**68. Agromyzidae** (Fig. 39.32A). Mostly small or minute flies. Thirteen genera are represented here, but some 80% of the species are endemic. Another 16% occur in adjacent countries; but only 5 species are considered to be recent introductions. The larvae are leaf- or stem-miners and gall makers. Larvae of several species occur on cultivated plants, and are important economically, whilst those of *Ophiomyia lantanae* live in the developing fruit of lantana and reduce the quantity of seed set by that weed. [Spencer 1978]

**69. Fergusoninidae** (Fig. 39.32B). The family, established by Hennig (1958), includes only the interesting genus *Fergusonina*. Though mainly Australian, it occurs

also in India and New Britain. Larvae live in leaf, bud and stem galls on myrtaceous plants (particularly *Eucalyptus*), in a remarkable association with nematodes of the genus *Fergusobia*. As the galling may prevent flower production and setting of seed, some species are of importance to the honey and timber industries. [Currie 1937]

**70. Xenasteiidae** (Tunisimyidae) (Fig. 39.32E). Minute flies with reduced venation, somewhat resembling Carnidae. Anepisternite bare. Cells M and discal open; CuA+1A absent. Male postabdomen with large T6 and S8; S6 and S7 lateral. Female with separate cerci; spermathecae 2, without differentiated cap. They occur mainly on tropical coasts of the Old World and Pacific; their biology and habits are unknown. [D. E. Hardy 1980; Papp 1980]

**71. Carnidae** (Figs 39.32C, D). Though often included in Milichiidae, this group is evidently not closely related. Specialised genera such as *Meoneura* (subfamily

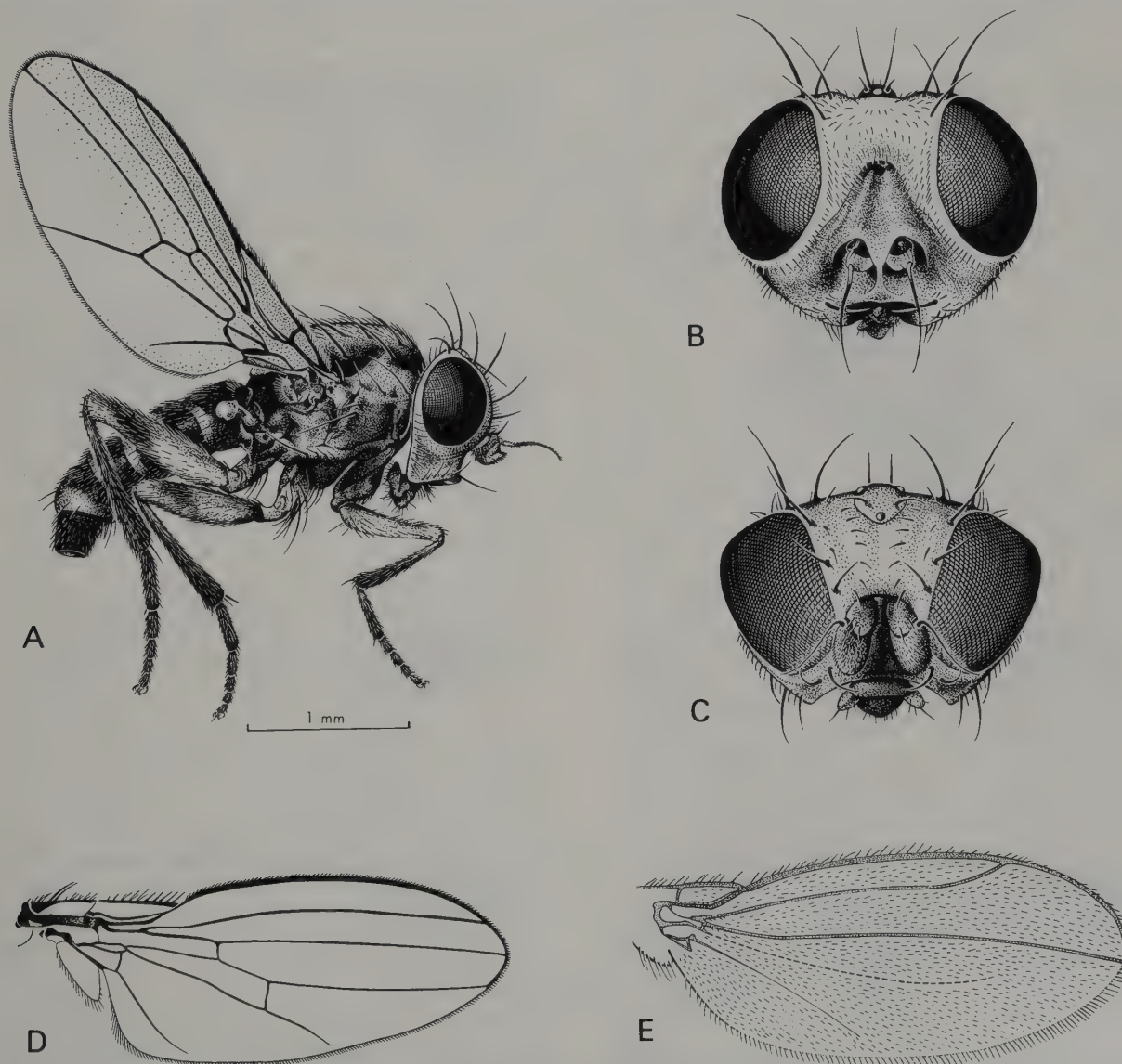


Fig. 39.32 A, *Cerodontha robusta*, Agromyzidae, ♀; B, *Fergusonina* sp., Fergusoninidae; C, *Australimyza* sp., Carnidae, head; D, same, wing; E, *Xenasteia* sp., Xenasteiidae. [A–D by T. Binder; E by S. P. Kim]

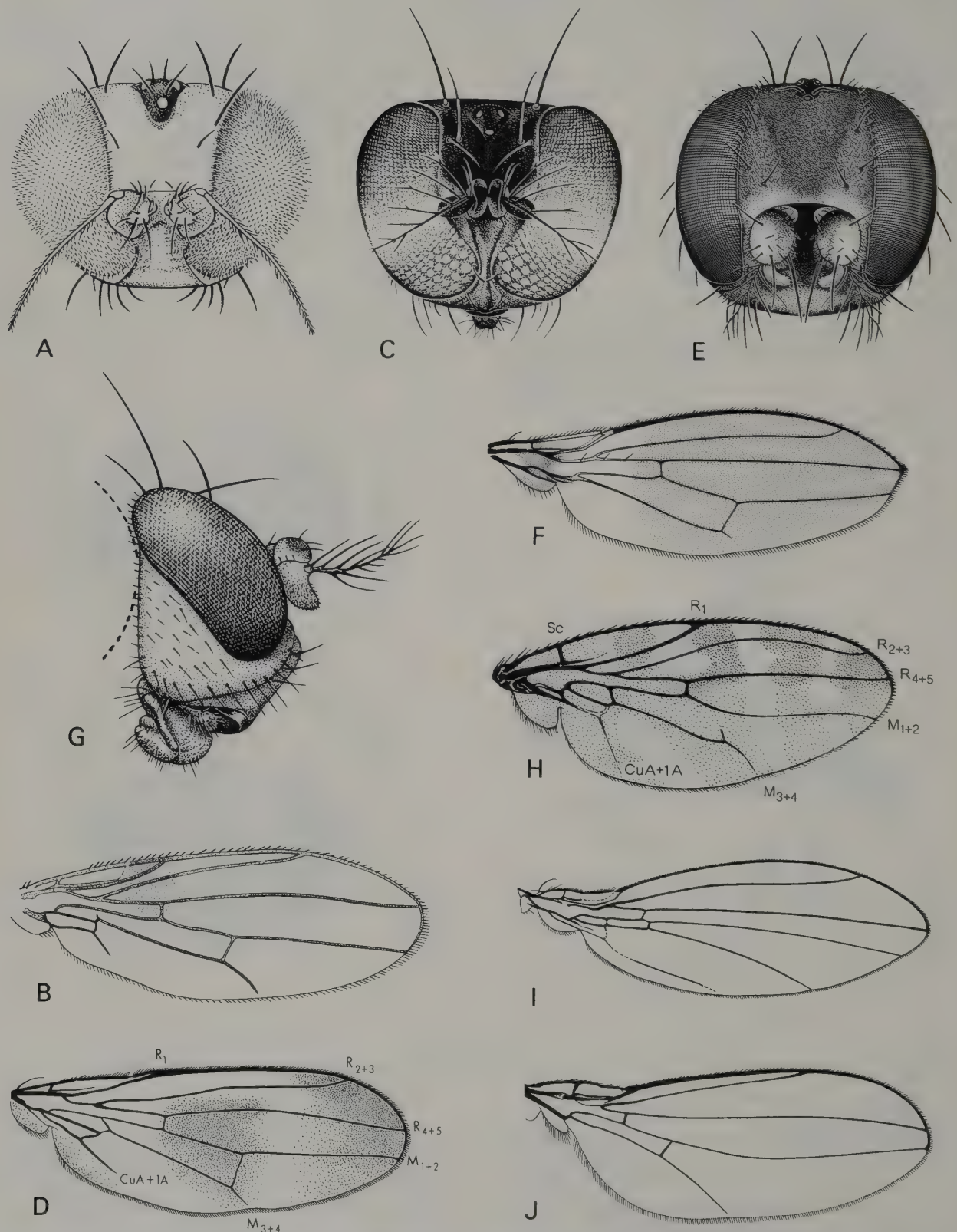


Fig. 39.33 A, *Nemo centriseta*, Aulacigastridae, head; B, same, wing; C, *Cyamops* sp., Periscelididae, head; D, same, wing; E, *Neurochaeta inversa*, Neurochaetidae, head; F, same, wing; G, *Periscelis* sp., Periscelididae, head; H, same, wing; I, Teratomyzidae, undescribed; J, *Leiomyza nitidula*, Asteiidae. [A, B, E, F by S. P. Kim; C, D, I, J by T. Binder; G, H by B. Rankin]



Carninae, recently reported from New Zealand) resemble Milichiidae through reduction of the protandrium and wing venation, but may generally be distinguished by having CuA+1A more distinct than 2A. In more primitive forms (*Hemeromyia*, *Australimyza*) CuA is very long, and male S6 and S7 are asymmetrically placed. Cerci of ♀ fused; spermathecae 2, sclerotised, with sclerotised cap. The predominantly Holarctic family is represented in Australia by a minute species of *Australimyza* (subfamily AUSTRALIMYZINAE) occurring on stranded debris on the shores of sheltered inlets.

### Superfamily ASTEIOIDEA

Size small to minute; habitus usually slender; face more or less sclerotised (weakly so in some forms), with distinct lower margin separating it from subcranial region; lower part of face more or less inflexed and visible in ventral aspect; vibrissae usually present; legs not greatly lengthened; tibiae without preapical dorsal bristles; costa generally without break just beyond humeral cross-vein; Sc variably reduced distally; cell CuP, when distinct, not of the drosophilid kind (see under Ephydroidea); distal section of CuA+1A short (except in Teratomyzidae); cerci of female separate.

**72. Neurochaetidae** (Figs 39.33E, F). Small, slender, more or less flattened, cursorial flies with hind femur enlarged, fore femur short and thick, mid femur short and slender; antennal segment 2 dorsally slit; prosternum much reduced. *Neurochaeta inversa* (upside-down fly) lives on *Alocasia macrorrhizos* in all stages (D. K. McAlpine 1978c). It is remarkable for its consistent orientation with the head downwards when on a vertical surface; it runs backwards as well as forwards. The aberrant clawless *Nothoasteia* is very little known. [D. K. McAlpine 1988]

**73. Periscelididae** (Stenomicroidae; Figs 39.33C, D, G, H). Face sclerotised, convex or protuberant medially; one or 2 fronto-orbital bristles present; antenna with segment 2 dorsally slit, segment 3 deflexed, and arista plumose. The genera *Periscelis*, *Cyamops* and *Stenomicroa*, occur in wetter forests of the eastern states, *Cyamops* extending to Tas. The larvae of *Periscelis* are recorded from wounds in tree-trunks, and those of *Stenomicroa* probably live mainly in phytotelmata of monocotyledonous plants. [Khoo 1984]

**74. Teratomyzidae** (Fig. 39.33I). Face sclerotised; postvertical bristles small, slightly divergent to convergent; vibrissae present; antenna porrect with segment 3 usually subcircular; palps short or vestigial. Prosternum reduced, without precoxal bridges. Wing narrow, costa broken at end of Sc, weakened near humeral vein, not reaching M<sub>1</sub>; cell CuA complete; alula vestigial. Protandrium symmetrical, segment 6 with complete tergite and sternite.

The family is widely distributed in the Oriental and Australian regions, also in South America. Adults rest mainly on ferns in cool forests, feeding on microflora of the frond surface. The Australian fauna includes undescribed species of both major groupings: the *Teratoptera* complex with distinct palps and deep subscutellum; and

the *Teratomyza* complex with vestigial palps and subscutellum. Larvae of the first grouping have been found on fronds of bracken (*Pteridium aquilinum*); the puparium is formed without visible change of the larval cuticle, and retains the median dorsal series of rough processes.

**75. Aulacigastridae** (Figs 39.33A, B). Face sclerotised, broadly convex; one reclinate and one more or less proclinate fronto-orbital bristle usually present; palps short; antenna porrect, without dorsal slit in segment 2, segment 3 short and deep; costa broken only at end of (desclerotised) Sc which is well removed from end of R<sub>1</sub>; CuP complete, vein CuA+1A extending beyond it. The minute adults of *Nemo* (Australia and New Guinea) are found on smooth *Eucalyptus* trunks and on leaves of *Alocasia*. This genus is related to the South African *Ningulus*. [D. K. McAlpine 1983]

**76. Asteiidae** (Fig. 39.33J). Small to minute flies with reduced venation. The larvae of *Leiomyza* have been found in fruiting bodies of fungi in Europe. The genera *Leiomyza*, *Phlebosotera*, *Astiosoma* and *Asteia* occur in Australia. [Sabrosky 1956]

**77. Anthomyzidae**. Vibrissae present; postvertical bristles usually convergent; face usually lightly sclerotised; antennal segment 2 without dorsal slit; segment 3 directed ventrally, with coarse hairs on anterior margin; prosternum broad without precoxal bridges. Most species occur in the Holarctic Region, but *Amygdalops*, widespread in the Old World tropics, lives in northern Australia. Its biology is unknown, but larvae of some other anthomyzids live in grass stems.

### Superfamily EPHYDROIDEA

Postvertical bristles convergent, or replaced by the divergent postocellar bristles (some Ephydriidae), or absent; vibrissae usually present. Antenna (except in Cryptochetidae) with segment 2 more or less cap-like, with dorsal slit on distal part; segment 3 with basal dorsal prominence concealed in recess of segment 2. Prosternum with precoxal bridges (weak in some minute forms). Costa broken at end of Sc, which is usually obsolete distally or fused with R<sub>1</sub>; CuA+1A, when present, short and arising preapically from posterior side of cell CuP. Male postabdomen symmetrical, with reduced segmentation. Female postabdominal segments short; cerci usually free. The Camillidae, Campichoetidae and Diastatidae are not known in Australia.

**78. Ephydriidae** (Risidae; Figs 39.34A, B). These flies are often found near water, both salt and fresh, but certain species of *Hydrellia* and *Scatella* occur on grasslands and lawns far from water. The larvae are mainly aquatic, or live within the stems and shoots of plants, often of aquatic plants; some feed on blue-green or other unicellular algae. *Hydrellia tritici* is generally the most abundant fly in extra-tropical pastures, and is associated with both land and freshwater plants. Adults of *Rhynchopsilopa* spp. attack and suck juices from ants of the genus *Crematogaster*, without necessarily killing their victims (Freidberg and Mathis 1985). [Cresson 1948; Bock 1987]

**79. Curtonotidae** (Figs 39.34F, G). Thorax usually subspherical, very convex above. Each tibia with one

preapical dorsal bristle and hairs in longitudinal rows. Wing often glassy, with reduced microtrichiation; a vein-like thickening extending distally from transverse section of CuA. Adults of *Axinota pictiventris* often hover over low vegetation in the wet tropics. [Wirth 1977]

**80. Drosophilidae** (Figs 39.34D, E). Distinguished mainly by the position of the reclinate fronto-orbital bristle near the eye and absence of a mesopleural bristle. The larvae of most species are fungivorous, some eating yeasts in decaying fruit; others have been recorded from fallen flowers, in faeces or urine, in museum formalin tanks, in leaf mines, or as predators/parasitoids of Hemiptera. The family is widely distributed, but there is a

concentration of species in north-eastern Qld. Though drosophilids are termed 'fruit-flies' by some geneticists, that name should be restricted to the Tephritidae. [Bock 1982]

**81. Cryptochetidae** (Fig. 39.34C). Small stout flies; costa twice broken; cell M confluent with discal cell. *Cryptochetum* has the arista much reduced and the major bristles of head undifferentiated. The larvae are endoparasites of mealy bugs of the family Margarodidae, and some are of economic importance. *C. monophlebi* and *C. iceryae* are Australian species which were introduced to California many years ago to control *Icerya purchasi*. The little known *Librella* has well-developed cephalic bristles

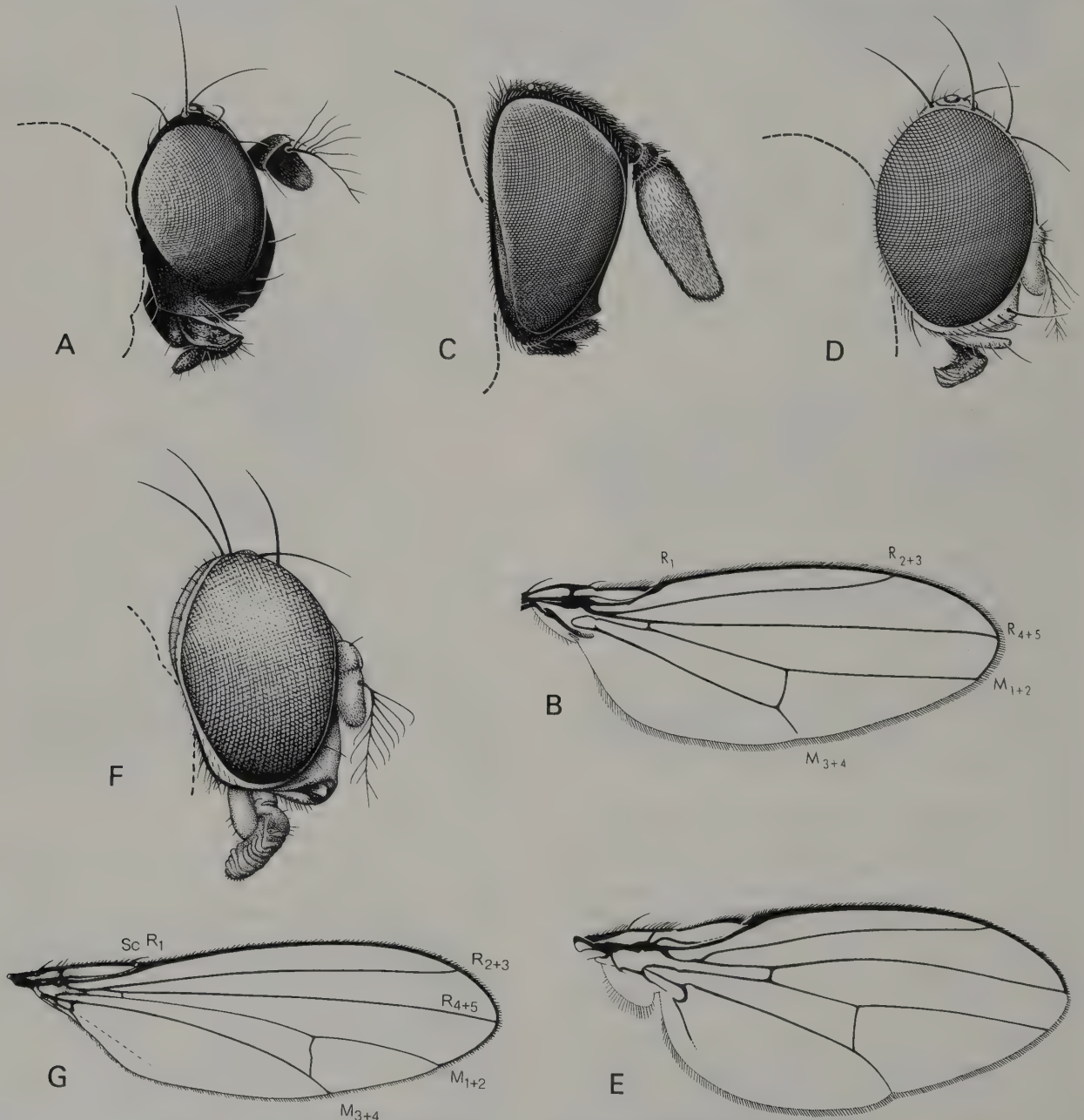


Fig. 39.34 A, *Hydrellia tritici*, Ephydriidae, head; B, same, wing; C, *Cryptochetum monophlebi*, Cryptochetidae; D, *Leucophenga albofasciata*, Drosophilidae, head; E, same, wing; F, *Axinota pictiventris*, Curtonotidae, head; G, same, wing. [A–E by T. Binder; F, G by B. Rankin]



and normal arista. Its position in the family depends on interpretation of the European Tertiary fossil *Phanerochaetum*. [Malloch 1927; D. K. McAlpine 1976]

### Superfamily CHLOROPOIDEA

Usually small compact flies, resembling those of the last superfamily. Antenna with segment 2 not cap-like, without dorsal slit. Prosternum usually with precoxal bridges. Costa generally broken at end of Sc; CuA+1A absent or desclerotised and arising from posterodistal angle of cell CuP; vein 2A usually more distinct than CuA+1A; or, in Chloropidae, venation of cubito-anal region much simplified (Fig. 39.35G). Protandrium with only one dorsal sclerite (sometimes asymmetrical) between T5 and epanandrium, apparently consisting of T6 fused with S6 and S8. Females with 2 spermathecae, which, in Milichiidae and Chloropidae, lack sclerotised vesicles.

**82. Tethinidae** (Figs 39.35E, F). Very small flies; postvertical bristles usually convergent, often with a pair of divergent postocellar bristles in front of them; 1 to 4 fronto-orbital bristles reclinate or sloping outwards, often also an inner row of incurved setulae on orbits; vibrissae present, anepisternite with one or more posterior bristles

and an upwardly directed bristle near upper margin; costa broken only at end of Sc. Larvae appear to be mainly associated with stranded seaweed and other shoreline debris. Only those of the subantarctic *Apetaenus* and *Listriomastax* have been described (Ferrar 1987, under Coelopidae). *Dasyrhicnoessa* is abundant in mangroves, whereas adults of *Tethina* and *Pseudorhichnoessa* are found on beaches or adjacent dunes.

**83. Canacidae** (Figs 39.35C, D). Closely related to Tethinidae, differing in the absence of convergent postvertical bristles. Fronto-orbital bristles usually flexed outwards over eyes; vibrissae usually weak or inserted behind vibrissal angle; face usually with a bulbous carina; male with compound penultimate abdominal segment (segments 6–8) at least as long as segment 5 (shorter or absent in Tethinidae); size small or minute. Except for a few foreign species inhabiting mountain streams, the family is confined to the sea shore and estuaries, the adults and larvae frequenting the intertidal zone. The genera *Isocanace*, *Nocticanace*, *Trichocanace*, *Xanthocanace*, *Chaetocanace* and the aberrant *Zalea* are represented in Australia. [Mathis 1982; D. K. McAlpine 1985]

**84. Milichiidae** (Phyllomyzidae; Figs 39.35A, B).

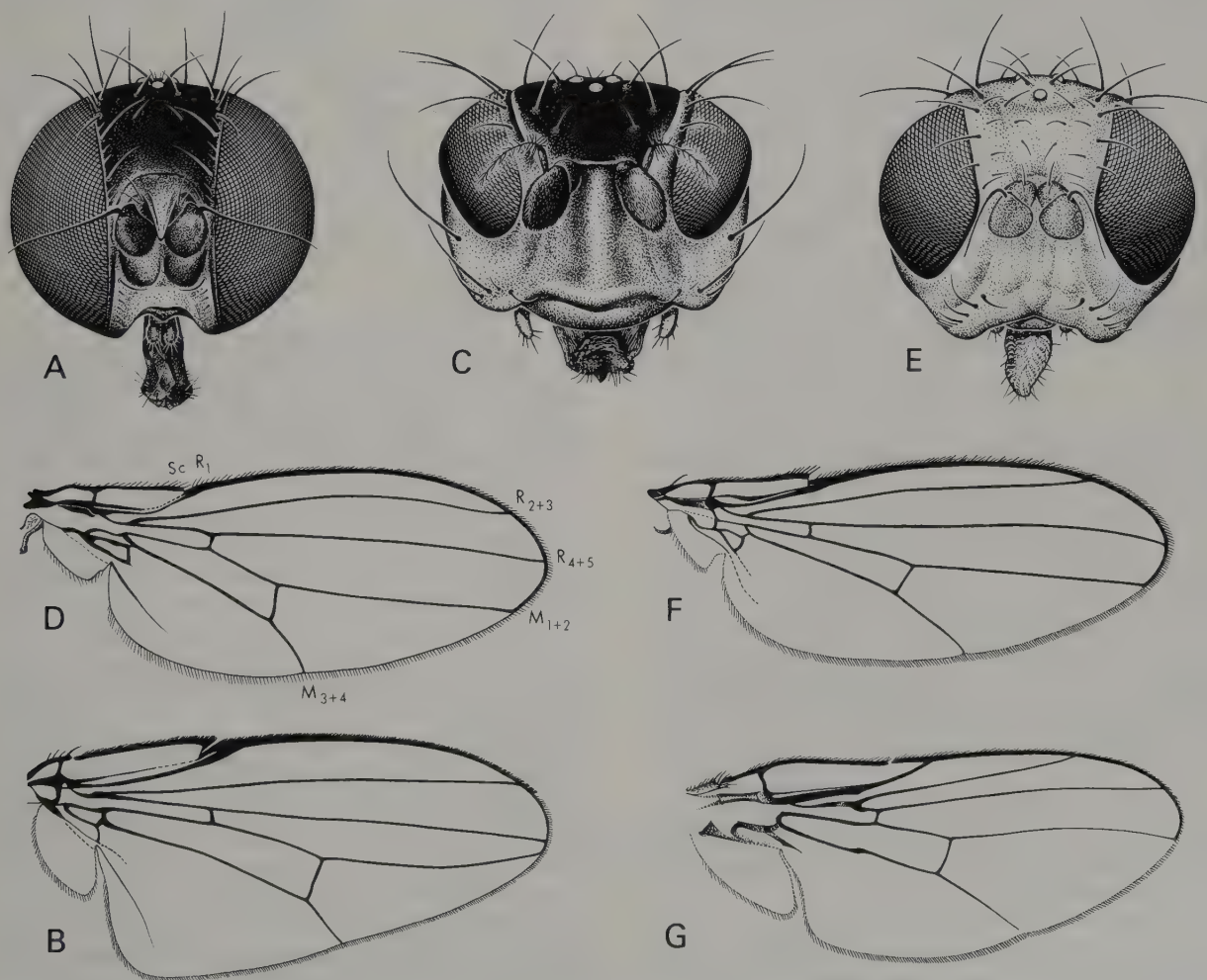


Fig. 39.35 A, *Milichiella* sp., Milichiidae, head; B, same, wing; C, *Isocanace albiceps*, Canacidae, head; D, same, wing; E, *Tethina nigriseta*, tethinidae, head; F, same, wing; G, *Batrachomyia* sp., Chloropidae. [T. Binder]

Postvertical bristles convergent or parallel; lower fronto-orbital bristles incurved (sometimes reduced to hairs), upper ones otherwise directed; vibrissae present; prosternal bridges present, or the prosternum reduced; costa twice broken; cells M and CuP closed; protandrium consisting of a single sclerite situated dorsally. Larval habits are varied; in Australia the larva of *Milichia piscivora* has been found in dead fish and that of *Milichiella* sp. in soil on rotting wood. Adults of *Desmometopa* have been observed 'cleaning' araneid spiders after the latter have fed.

**85. Chloropidae** (Oscinidae; Siphonellopsidae; Fig. 39.35G). Postvertical bristles usually convergent (subparallel in some Chloropinae); fronto-orbital bristles usually weak, never with distinct proclinate and reclinate elements; prosternum with well-developed precoxal bridges; mesopleural bristle absent. The adults are of almost ubiquitous occurrence, and the larvae inhabit a wide range of habitats, though still little known. Larvae of numerous species live within the young shoots and stems of grasses and other plants; these may be largely bacterial feeders.

In the N.T., larvae of *Anatrichus* are associated with rice, but it is uncertain if they are the primary cause of damage. Larvae of *Batrachomyia* live beneath skin of frogs, feeding on blood. *Gaurax flavoapicalis* has been reared from both new and rotting swedes. Larvae of *Gaurax* spp. (with adults very like the last) live in spider egg-cocoons, while *Gaurax tonnoiri* has been reared from cocoon masses of sawflies and oothecae of mantids. Larvae of *Gaurax luteohirtus* are recorded by J. W. Evans (1931) as eating the eggs of *Eurymela fenestrata* (HEMI), and some species of *Apotropina* are parasites or hyperparasites within the burrows of fossorial Hymenoptera. *Cadrema nigricornis flavus* has been reared from stranded marine molluscs. [Spencer 1986]

### Superfamily BRAULOIDEA

This includes only one very small family of flies which are so highly modified as to render their relationships obscure. It is certain that there is no connection with the Phoridae or the pupiparous muscoid families.

**86. Braulidae.** Wingless, flattened, highly specialised flies, with vestigial eyes, tarsi broadened distally, and comb-like claws. The bee louse, *Braula coeca*, a widely distributed species, has been introduced into Tas. Adults are usually found upon honey bees, whilst the larvae live in cells of that species. They pupate without any modification of the larval cuticle (as in Teratomyzidae). [Grimaldi and Underwood 1986]

### Superfamily MUSCOIDEA

Includes all the 'calyptate' families of Schizophora and several greatly modified, but probably related, parasitic families (Hippoboscidae, etc.).

**87. Anthomyiidae** (Fig. 39.36C).  $M_1$  not curved forward distally. The complete vein CuA+1A occurs otherwise among the calyptate families only in the Scathophagidae, an exotic group often included in the Anthomyiidae. The larvae of a species of *Fucellia* live in

stranded seaweed on beaches. *Delia platura* is a cosmopolitan pest species, its larvae damaging seedlings of onions, beans and other plants. [Colless 1982]

**88. Fanniidae.** Poorly represented in Australia, by some 11 species in 3 genera, one of them endemic. They include the relatively innocuous lesser house fly, *Fannia canicularis*, of which the adults occur in numbers in houses and the larvae live in organic refuse. [Pont 1977]

**89. Muscidae** (Figs 39.2K, 3D, 6B, 36A, B). A large and variable family, with many species of economic and medical importance.

A key to subfamilies was given by Malloch (1925), but concepts have changed greatly in recent decades (see Hennig 1965; Pont 1989). We are unable to present the often complex basis for the current subfamily classification in a simple key. The Muscinae (including Stomoxyinae), Phaoniinae (including Egiiniinae), MYDAEINAE and Coenosiinae (including Lisperinae) occur in Australia.

Adults of *Lispe* (COENOSIINAE) generally occur near fresh or salt water; the larvae are probably mainly aquatic and the adults predacious. The Coenosiinae also include *Coenosia* and *Pygophora*, which are common in grasslands and gardens. The adults are predacious on smaller insects.

In the large subfamily PHAONIINAE, most larvae are predacious on other insect larvae, particularly those of Diptera. They occur in very diverse habitats. The larvae of *Limnophora nigriorbitalis* live in moss at the margins of streams, where they are frequently submerged. Those of other species live in decaying fruit and other vegetable matter, fungi, manure and carrion, while those of *Atherigona* have also been found boring in the stems of such grain crops as millet. The larvae of *Ophyra* are predators in carrion.

The most familiar species of Muscini (MUSCINAE) is the house fly, *Musca domestica*, which carries many kinds of pathogenic bacteria affecting humans and domestic animals. The adults, which tend to congregate in human dwellings, are attracted to both wet and dry organic foods, including much that is to be eaten by humans. The larvae live in excrement of various animals and other organic refuse. The bush fly, *Musca vetustissima* (Fig. 39.36A), is a constant worry to humans and domestic animals in the open air during summer (for its biology, see Hughes *et al.* 1972). The larvae of *Passeromyia* occur in nests of many species of birds, either as parasites sucking the blood of the nestlings, or merely as scavengers.

The Stomoxyini (Muscinae) include blood-sucking flies with the prestomal teeth of the labella adapted for piercing (Fig. 39.3D). The cosmopolitan stable fly, *Stomoxys calcitrans*, bites humans and domestic animals, particularly horses and zoo animals. Its larvae normally live in horse manure mixed with straw, etc. The buffalo fly, *Haematobia exigua*, which was introduced from the Oriental Region, is now a major pest of cattle and horses in the northern half of Australia. [Crosskey 1962a; Pont 1972; Ferrar 1979; Skidmore 1985; and see Skidmore's references to Paterson and Norris, Pont, Vockeroth]



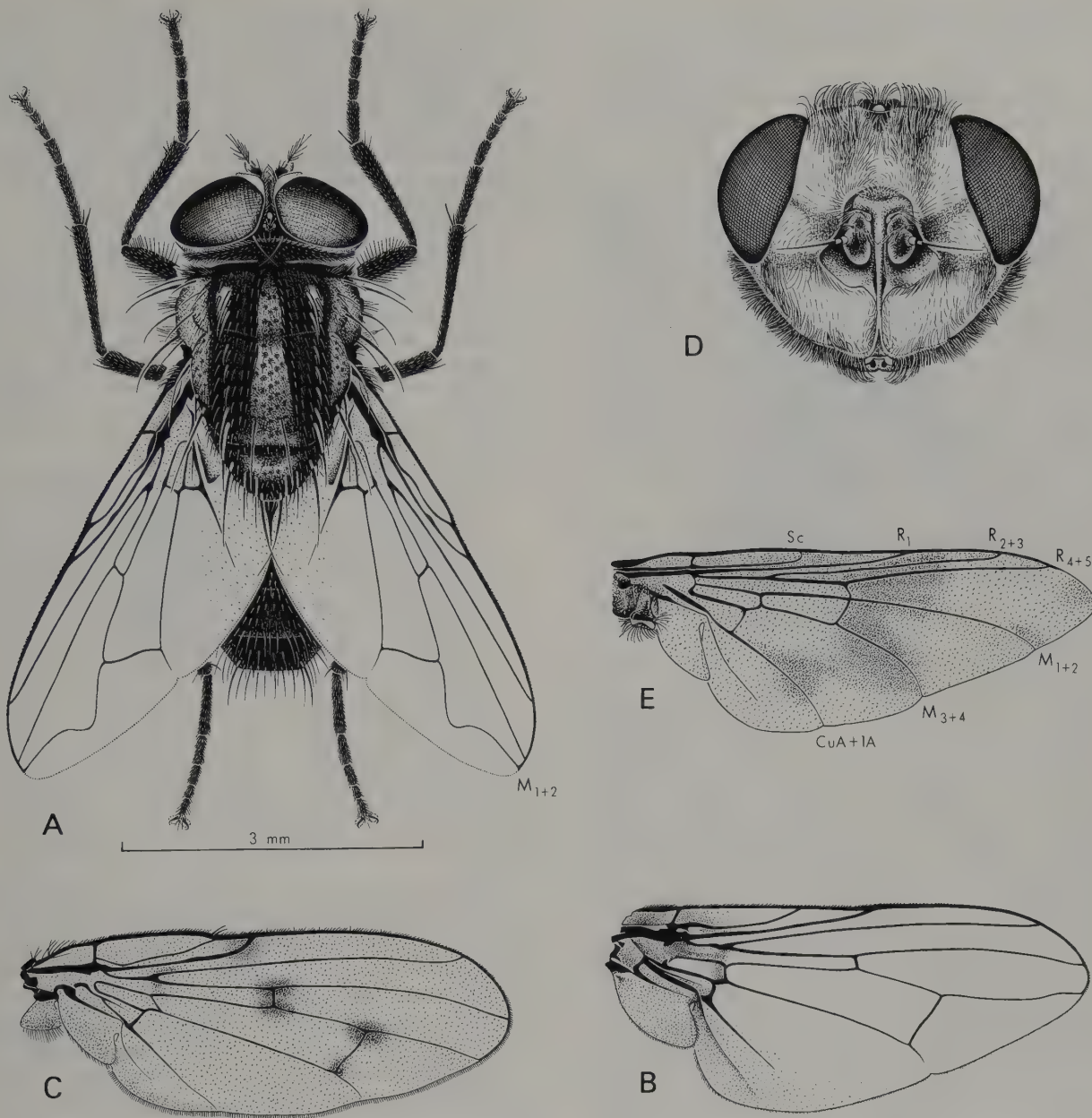


Fig. 39.36 A, *Musca vetustissima*, Muscidae, ♂; B, *Ophyra rostrata*, Muscidae; C, *Anthomyia punctipennis*, Anthomyiidae; D, *Gasterophilus intestinalis*, Gasterophilidae, head; E, same, wing. [T. Binder]

**90. Calliphoridae** (blowflies, bluebottles; Figs 39.3E, 7C, 9B, 10C, 11C, 37B). A large, cosmopolitan family of flies, mostly stoutly built and of moderate size; almost all have the antennal arista plumose. They vary considerably in details of structure, and several well-marked subfamilies can be recognised.

*Key to the Subfamilies of Calliphoridae Known in Australia*

1. Anterior lappet of metathoracic spiracle with tuft of long, fine hairs towards dorsal margin; subscutellum distinct; face almost always with strong carina between antennae ..... AMENIINAE

- Anterior lappet of metathoracic spiracle bare, or without long hairs; subscutellum and facial carina rudimentary or absent ..... 2
- 2(1). Stem-vein (extreme base of R) with row of hairs posteriorly ..... 3
- Stem-vein bare ..... 4
- 3(2). Lower calypter haired on upper surface; external posthumeral bristle absent; arista strongly plumose ..... CHRYSOMYINAE
- Lower calypter bare on upper surface; usually with a posthumeral bristle placed laterally to level of presutural bristle; arista rather weakly plumose or pubescent only ..... RHINIINAE
- 4(2). With an external posthumeral bristle placed laterally to

- level of presutural bristle; sternopleural bristles usually 2:1 (if 1:1, 3 notopleural bristles present) .....  
 ..... CALLIPHORINAE  
 Without any such external posthumeral bristle; sternopleural bristles 1:1 ..... POLLENIINAE

Adult calliphorids are ubiquitous, flying mainly by day, although a few species appear in light traps. They are strongly attracted to moisture, and feed mainly on nectar, honeydew and other sweet liquids, and on the liquid products of organic decomposition; the last provide the proteins essential for egg maturation. Reproduction is oviparous or ovoviviparous. Many species, particularly in the Calliphorinae and Chrysomyinae, breed in carrion, although at least some species of *Calliphora* parasitise earthworms (Fuller 1933). By contrast, the Polleniinae are probably all parasites of earthworms, the larvae of at least some Rhiniinae live in the nests of ants or termites, and the Ameniinae are parasites of land snails.

Although their numbers sometimes reach plague proportions, blowflies are far less important than other groups of flies as domestic nuisances or vectors of disease. However the larvae of some species are responsible for the cutaneous myiasis of sheep, known as 'blowfly-strike', which annually causes direct and indirect losses of millions of dollars to the Australian sheep industry (review by Norris 1965). This myiasis is an extension of the carrion-breeding habit, and is initiated by only a few species, the 'primary flies'. These are attracted to oviposit on areas of the sheep's body, usually where persistent wetting of the wool by urine, sweat or rain has caused 'scalding' of the skin and superficial bacterial infection. The younger larvae feed on serous exudates, but the older larvae attack the living tissues, producing extensive lesions and sometimes death of the sheep. Once the strike is established, other 'secondary' species may be attracted to extend the infestation. A group of 'tertiary flies' is also recognised—their larvae occur in healing scabs. In Australia, some 80% of primary strikes are caused by the introduced, metallic green sheep blowfly *Lucilia cuprina*. The related *L. sericata*, of importance in some other countries, also occurs here but is practically innocuous. The other important primary flies are native species of *Calliphora*, notably *C. augur* in south-eastern Australia and *C. nociva*, which replaces it in the drier inland and western areas. The most important secondary fly is *Chrysomya rufifacies*, whose 'hairy maggots' not only compete with, but actively prey upon, the primary maggots. A similar type of succession occurs in carrion, but with the primary flies playing a much smaller role. The Oriental screw-worm fly, *Chrysomya bezziana*, also causes a serious wound-myiasis, with consequent economic losses in livestock. Although not yet present in Australia, it is widespread in Asia and on the island of New Guinea and its possible introduction poses a serious threat to our cattle industry (Norris and Murray 1964).

The family is well developed in Australia. Some 4% of our species are immigrants, while the Ameniinae, Rhiniinae and Chrysomyinae tend to be distributed mainly in the north, and show other evidence of relatively

recent entry from that direction. By contrast, *Calliphora* (66 spp.) and *Pollenia* (29 spp.) seem to have undergone considerable radiation in the more humid, temperate areas; their origins, and relationships with other faunas, remain obscure. The striking metallic green and blue Ameniinae, formerly regarded as prosenine Tachinidae, were transferred to the Calliphoridae by Crosskey (1965). [G. H. Hardy 1940; Paramonov 1960; Norris 1965, 1973; Dear 1977]

**91. Sarcophagidae** (flesh flies; Fig. 39.37A). A cosmopolitan family, treated by some authors as a subfamily of Calliphoridae, but forming a fairly compact group defined by the characters given in the key. All species are viviparous or (rarely) ovoviviparous, with a bilobed uterine pouch. The larvae of most species have the posterior spiracles set in a deep pit or chamber. Two subfamilies occur in Australia:

- Arista plumose; thorax with 3 broad, longitudinal, dark stripes (very faint in *Tricharaea*); abdomen with changing, tessellated pattern of silvery-grey and black patches; usually 4 notopleural bristles; sternopleural bristles 1:1:1 or 2:1 ..... SARCOPHAGINAE  
 Arista bare, or nearly so; thoracic pattern variable; abdomen usually with silvery-grey, pruinose bands; usually only 2 notopleural bristles; sternopleural bristles 1:2-4 ..... MILTOGRAMMATINAE

The MILTOGRAMMATINAE, although widely distributed, are most common in the drier inland areas. As far as is known, the larvae live as food-parasites in the nests of solitary wasps and bees, generally those of fossorial species. Seven genera are recorded from Australia, of which *Protomiltogramma* seems to be by far the commonest.

The SARCOPHAGINAE are ubiquitous, commonly seen on foliage or around carrion. Almost all species are viviparous, usually depositing their larvae on some type of decomposing organic matter, and in northern areas certain species are common primary or secondary breeders in carrion. The family is very rarely involved in myiasis, animal or human, in Australia, although species of considerable medical importance occur in other countries. The genus *Blaesoxipha* is interesting, in that the known larvae are all parasites of Acrididae. Likewise, larvae of 3 species of *Baranovisca* (or *Parasarcophaga*) are known to live in egg-cases of spiders and feed on the developing eggs. Other genera also have been bred from insects and snails, but at least some of these are necrophagous, rather than truly parasitic. The dominant genera in Australia are *Sarcorohdendorfia* (= *Tricholioproctia*) and *Parasarcophaga*, which together make up more than half our fauna in this subfamily. A number of species are extralimital, e.g. the cosmopolitan *P. crassipalpis*, and *Tricharaea brevicornis*, a presumably recent immigrant from South America, now widespread in south-eastern Australia. [Souza Lopes 1959; Souza Lopes and Kano 1979; Cantrell 1978, 1981, 1986a; Malloch 1930]

**92. Unnamed family** (Figs 39.38c, d). Represented by a single unnamed taxon, currently under study and probably requiring a new family. It includes some 12 species that are characterised by the very broad orbital plates,



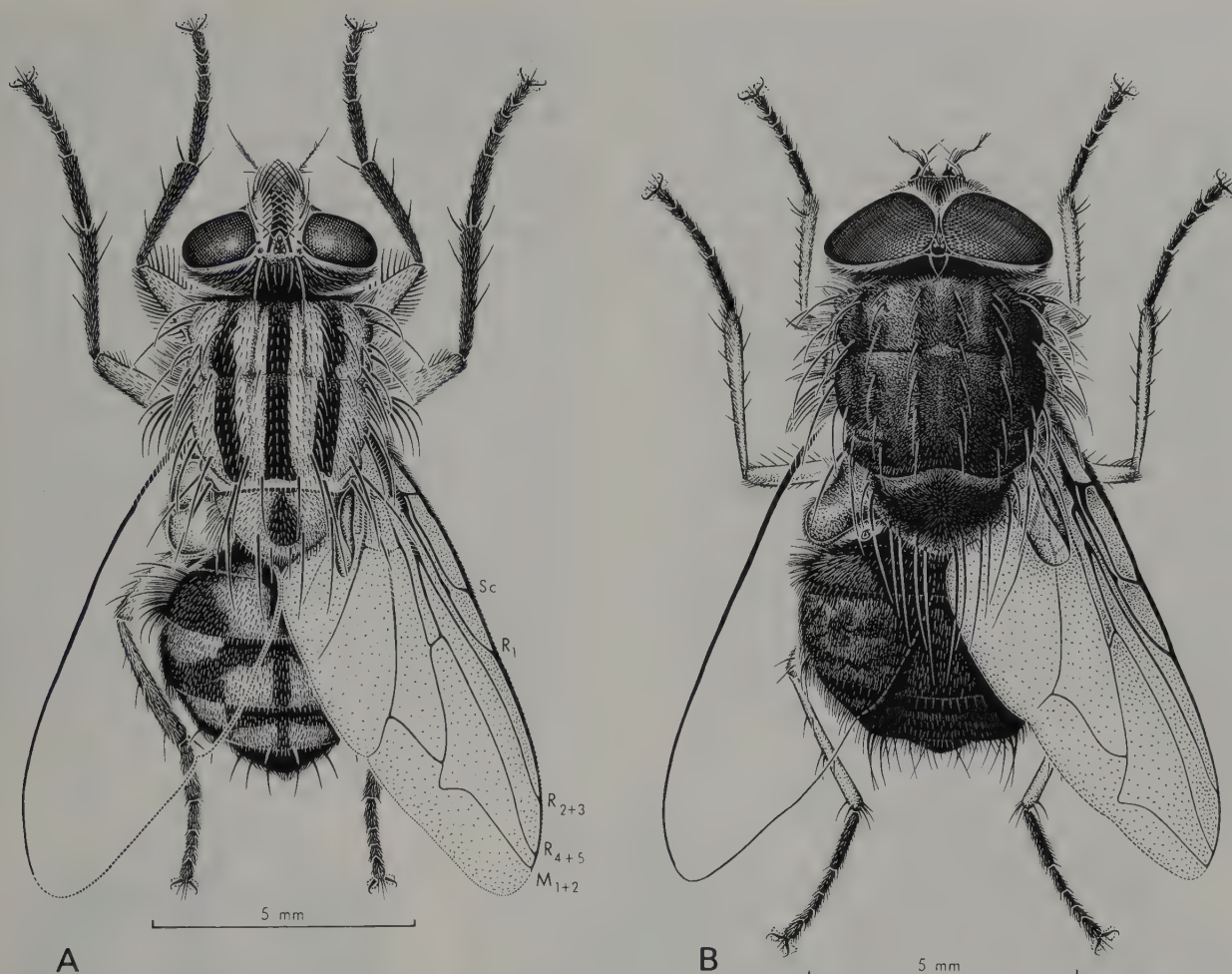


Fig. 39.37 A, *Sarcorohdendorfia hardyi*, Sarcophagidae, ♀; B, *Calliphora stygia*, Calliphoridae, ♂.

[T. Binder]

which often meet; by the greatly enlarged male antennal segment 3, which is shaped like an axe-head, in several species excavated to form 2 porrect, finger-like lobes (a New Guinea species has 3 lobes!); and by the robust, downcurved, spatulate oviscapt. The latter suggests parasitism, perhaps of some other arthropod or even a plant; but nothing is known in that regard. Male genitalia suggest some relationship to the exotic Rhinophoridae, but proper allocation of the taxon remains doubtful.

**93. Tachinidae** (Figs 39.5C, D, 38A). An immense and taxonomically difficult family, variously subdivided by different authorities. Current practice is to recognise only one family, defined mainly by the venation and the usually strongly developed subscutellum, with 4 or 5 subfamilies (see below). Most species are stout bodied, strongly bristled, and drab in coloration. They range in size from small species about half as big as a house fly, up to the large, showy species of *Rutelia* with wingspans of over 35 mm. Some, e.g. *Chaetophthalmus*, superficially resemble calliphorids or sarcophagids, whereas a few genera (e.g. *Cylindromyia*) are more elongate and include wasp-mimics.

The adults are ubiquitous, while their larvae are all endoparasitic in other arthropods, principally insects; a

possible exception is *Chrysopasta elegans*, reported to live as an inquiline in termite nests. Reproduction is oviparous or ovoviviparous, but life histories vary considerably in details. Some species lay their eggs or larvae directly on, or rarely in, the host, or deposit them in places frequented by the host, which is then sought out and penetrated by the young larva. Others lay numerous, tiny, 'microtype' eggs on the host's food plant; if ingested, they hatch and the larvae penetrate via the host's gut wall. During some part of their growth, the larvae are usually connected with the external atmosphere through a perforation in the body wall or a trachea, and the apex of the abdomen becomes enclosed there in a sclerotised 'funnel' formed by reaction of the host tissue. As a rule, the host eventually succumbs, and the parasite leaves to pupate in the soil; though species are known which pupate within the host, or, by feeding on non-vital tissues and retaining metabolic wastes within their bodies, leave the host while it is still alive.

The family includes parasites of many orders, but principally Lepidoptera, Coleoptera, Hemiptera and Orthoptera, including many pest species. No doubt, tachinids play an important role as natural regulators of insect numbers, though little seems to be known of their

real importance in this respect. They have been employed as biological control agents in some countries, but only to a very limited extent in Australia.

Although over 500 species have been recorded from Australia, our fauna is still very imperfectly known. The family is probably still actively radiating, and its members present an extraordinary range of taxonomic characters. This creates formidable problems in the delimitation of groups at all levels. Five subfamilies are recorded from Australia. The PHASIINAE, parasitic in Hemiptera, include species of atypical appearance, some with widened coloured wings and reduced chaetotaxy (*Alophora* spp.), as well as more normal forms. The DEXIINAE mostly have a strong facial carina and/or plumose arista and are parasitic in larval Coleoptera; others lack the carina but are otherwise similar. The Oriental-Australasian tribe Rutiliini includes many large species, often with brilliant metallic coloration (Plate 5, O, P), and the genus *Rutilia* is a prominent element of the Australian tachinid fauna. The TACHININAE and GONIINAE include many diverse forms, parasitic mainly in Lepidoptera. The present tribal classifications of both subfamilies are artificial and need to be redefined, but this will require information on life histories and host relationships, much of which is lacking.

The DUFOURIINAE, small species parasitic in adult Coleoptera, are now known to occur in Australia but none are described. [Cantrell 1983, 1985, 1986b, 1986c]

**94. Gasterophilidae** (Figs 39.36D, E). A small family, represented in Australia only by 3 introduced species of horse bot fly, *Gasterophilus intestinalis*, *G. nasalis* and *G. haemorrhoidalis*. The adults have vestigial mouth-parts, as in the Oestridae (also called bot flies, and with similar habits), but  $M_1$  is not curved forwards to meet  $R_{4+5}$ . All species are brown and rather bee-like, and *G. intestinalis* has patterned wings. The eggs are attached to hairs on the host's head or body, and the young larvae make their way to the horse's mouth, or are picked up by licking. They spend a period burrowing in the epithelial tissues of the mouth and tongue, and then pass to the stomach, where they attach to the mucous membrane, but the effect on the host appears usually to be slight. Eventually, they pass out in the faeces and pupate in the soil. Very rarely, the young larvae cause a 'creeping eruption' in human skin.

**95. Oestridae** (Fig. 39.38B). A small family of bot flies, related to the Tachinidae, but with vestigial mouth-parts and, in Australian genera,  $M_1$  meeting  $R_{4+5}$  well short of the wing margin. The larvae are parasitic in the nasal and respiratory passages of mammals. The intro-

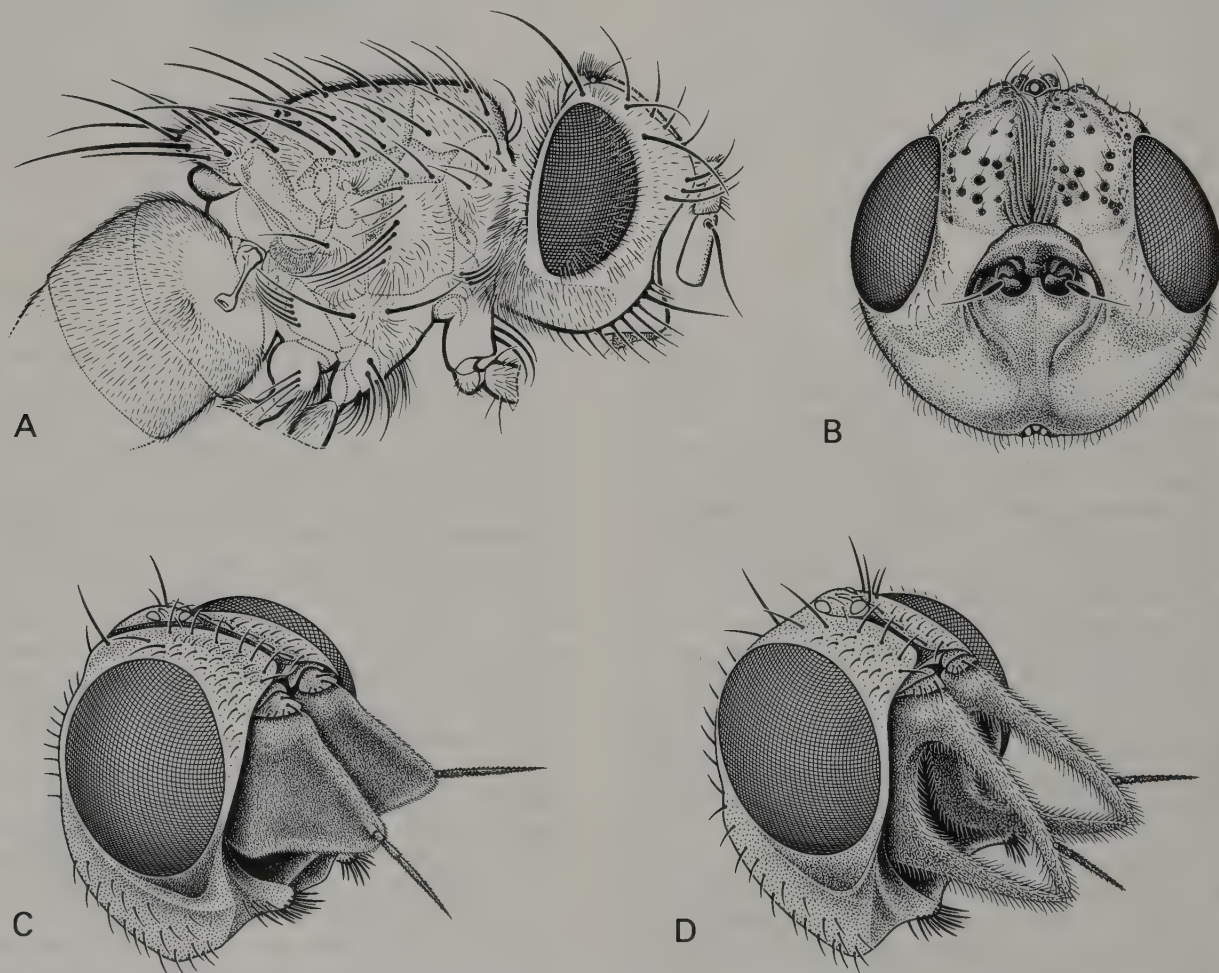


Fig. 39.38 A, *Chaetophthalmus* sp., Tachinidae; B, *Oestrus ovis*, Oestridae; C, D, ♂♂ of 2 undescribed species from undescribed family 92.

[A, B by T. Binder; C, D by S. P. Kim]



duced sheep bot fly, *Oestrus ovis*, is widespread in Australia, but apparently causes no serious disease. The female deposits young larvae around the sheep's nostrils; they develop in the nasal sinuses, and are sneezed out when mature, to pupate in the soil. Humans are sometimes infested, particularly in the eyes, in sheep-raising countries, but such cases are extremely rare in Australia. *Cephalopina titillator*, in feral camels, has a similar biology. There is only one known native oestrid, *Tracheomyia macropi*, whose larvae infest the trachea of the red kangaroo (*Macropus rufus*); the same, or a related, species occurs also in the euro (*Macropus robustus*). Little is known of its life history, but infestations can be common, with rates of up to 30% in some populations of *M. rufus* (Mykutowycz 1963). [Spratt 1984]

**96. Hippoboscidae** (louse flies, wallaby flies, keds; Fig. 39.39A). A family of greatly modified, blood-sucking flies, perhaps related to the blood-sucking muscids. The adults live as ectoparasites amongst the hair or feathers of mammals and birds, and, with their flattened bodies, porrect mouth-parts, and robust legs, have a characteristic louse- or tick-like appearance. The wings are well developed in most species, with the strong veins concentrated anteriorly. In several exotic genera, they are shed when the fly becomes established on its host, whereas a few other species have them reduced or, in *Melophagus*, vestigial. Reproduction is by adenotrophic viviparity and the

mature larvae are usually deposited away from the host, though in the sheep ked (*Melophagus ovinus*) they are laid and pupate in the host's wool.

In the large subfamily ORNITHOMYIINAE most species are restricted to avian hosts. However, *Ortholfersia* (4 spp.) and *Austrolfersia* (1 sp.) occur only in Australia, as parasites of wallabies and, doubtfully, of kangaroos. The other 2 subfamilies, which include only some 30% of hippoboscoid species, are almost exclusively parasites of mammals other than bats. Our species of HIPPOBOSCINAE and MELOPHAGINAE are all introduced. *Hippobosca equina*, occasionally imported on horses and cattle, does not appear to be established here, but *Melophagus ovinus*, often called the 'sheep tick', is common in cooler parts of the continent where heavy infestations sometimes cause losses through anaemia and staining of the wool. [Maa 1963b, 1969]

**97. Streblidae** (Fig. 39.39C). A small family of blood-sucking ectoparasites of bats, widely distributed in the tropics and subtropics. Their origins are obscure, and the New World subfamilies may have been independently evolved. Streblids show many features associated with the ectoparasitic habit: piercing mouth-parts, enlarged legs and claws, reduced sensory apparatus, specialised reproduction; but they have tended to retain functional wings, presumably used in finding a host. There are usually 2–8 individuals per bat, and most species show a

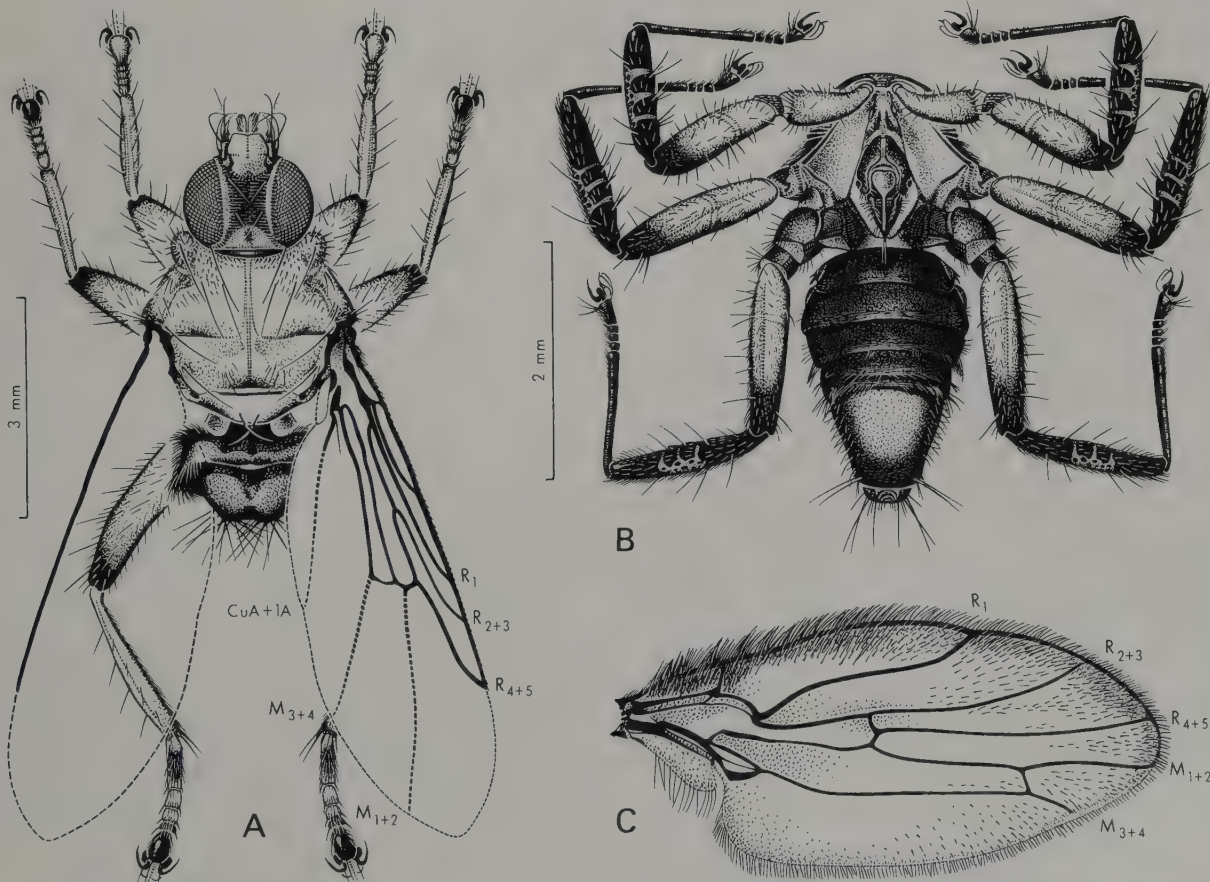


Fig. 39.39 A, *Ortholfersia macleayi*, Hippoboscidae, ♂; B, *Cyclopodia australis*, Nycteribiidae, ♀; C, *Brachytarsina uniformis*, Streblidae.

[T. Binder]

marked association with one family, and occasionally with one species of bat. Of the Old World subfamilies, the NYCTERIBOSCINAE are free-living in the host's fur, but in the ASCODIPTERINAE the female embeds itself in the subcutaneous tissue, and there degenerates to a sac-like organism enclosed in a cyst. Both reproduce by adelotrophic viviparity, the larvae developing one at a time and pupating on the floor of the roosting site. Both subfamilies occur in the warmer parts of Australia. The two most common species are extralimital, the large *Brachytarsina amboinensis* being widely distributed in the Oriental Region, and the small *Raymondia minuta* extending to New Guinea and the Solomon Is. [Maa 1971]

**98. Nycteribiidae** (Fig. 39.39B). A small but widespread family of blood-sucking ectoparasites, somewhat spider-like in appearance, and of obscure origins. As in the Streblidae, the adults inhabit the fur of bats, but their structure is more specialised. Legs and claws are very strongly developed, and the eyes reduced or absent, but all vestiges of wings have been lost, and the body is markedly flattened, particularly the thorax. They resemble the Streblidae also in mode of reproduction, except that the larvae are actively glued to the wall of the bat's roost by the larvipositing female. The puparium is oval and sometimes glossy black. Emergence of the adult is

apparently postponed until triggered by warmth or physical contact of a roosting bat in its immediate vicinity. Many species appear to be host specific, but, as also in the Streblidae, this may be at least partly due to the isolated roosting habits of some bats. However, the restriction of the very large species of *Cyclopodia* to the fruit bats may be an ancient adaptation. The Australian species belong in 6 genera, and are found wherever suitable hosts occur. Among the better known species are *Basilia falcozi*, widely distributed within Australia on cave-dwelling vespertilionid bats, and *Cyclopodia albertisii*, found on flying-foxes (*Pteropus* spp.). The latter is also widely distributed on islands to the north of Australia. [Maa 1971]

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# Trichoptera

(*Caddis-flies, caddises*)

A. NEBOISS

*With contribution by J. C. Dean*

Endopterygote Neoptera with reduced mouth-parts; two pairs of subequal functional membranous wings; fore wing with anal veins looped; body and wings more or less densely covered with hairs and occasionally with groups of scales. Larvae aquatic; mouth-parts with well developed mandibles, strongly developed functional legs and pair of abdominal prolegs; free living, constructing fixed shelters or portable cases. Pupae exarate with strong mandibles.

The Trichoptera, or caddis-flies, comprise one of the largest orders of aquatic insects, with a world fauna of more than 7000 species known to date. About 480 species representing 25 families are known from Australia.

Caddis-flies are holometabolous, and most closely related to the Lepidoptera. The adults (Fig. 40.1) are small to moderate-sized, winged insects with moth-like appearance and range from 2 to 40 mm in length. They have slender, filiform antennae and large compound eyes. Body, legs and wings are covered with fine hair. However, the structure of their mouth-parts and details of wing venation distinguish them from all but a few (e.g. Agathiphagidae) Lepidoptera. Most adults are drab and crepuscular, although a few are quite distinctly coloured and some are diurnal. Caddis-flies mate in flight, on the ground or on riparian vegetation. They are generally oviparous, and eggs are deposited in or near water shortly after mating. The larvae (e.g. Figs 40.11A, L, N) are aquatic, and morphologically resemble lepidopteran caterpillars, but lack prolegs on abdominal segments 1–8. They live not only in all types of freshwater habitat, but also in saline coastal lakes and streams (*Symphitoneuria*) and intertidal rockpools (*Philanisus*).

## Anatomy of Adult

**Head** (Figs 40.2A, C). Paired compound eyes well

developed, usually distinctly separated, but in some species almost meeting at the vertex (male *Marilia*) (Fig. 40.6C). Ocelli absent in most families, 3 when present, 2 in some Hydroptilidae. Antennae slender, multisegmented, filiform, seldom pectinate or serrate, about as long as, to noticeably longer than, fore wing; basal segment (scape) often more or less enlarged, sometimes modified in males. Antennal flagellum in Hydroptilidae reveals a variety of hair and sensilla forms (Wells 1984) (Fig. 40.3L), many of them characteristic of genera.

The mouth-parts are weakly developed, adapted for ingestion of liquid foods, more or less extended in Plecotarsidae, Kokiriidae and Stenopsychidae. Mandibles almost invariably vestigial; maxillae and galeae small or absent, labium somewhat larger. Maxillary palps 5-segmented, except in *Anisocentropus* (Calamoceratidae) which has 6 segments; males of many families with reduced number of segments; apical segment sometimes long, flexible, multiarticulate. Labial palps usually 3-segmented with apical segment often long and flexible.

Males may have hinged processes on frons between bases of antennae (some Conoesucidae); eversible scent-organs arising from vertex of head (some Hydroptilidae and Calocidae) (Fig. 40.3K); or pilifers on frons (certain Philorheithridae). Raised setiferous warts on vertex, between the bases of antennae or behind the eyes.



A



B



C



D



E



F



G



H



I



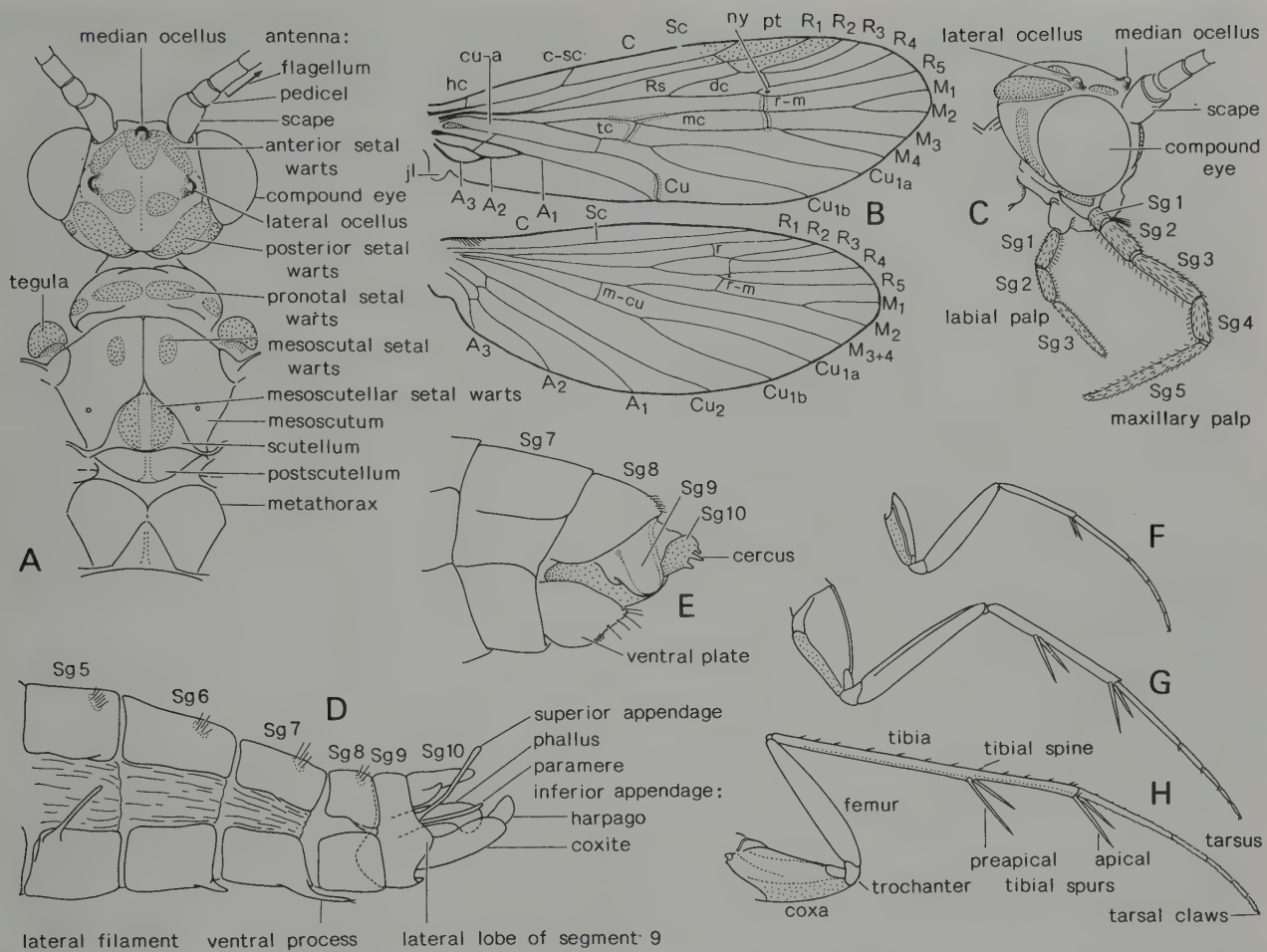


Fig. 40.2 Generalised adult Trichoptera: A, head and thoracic segments, dorsal; B, wing venation; C, head, lateral; D, terminal segments of ♂ abdomen, lateral; E, terminal segments of ♀ abdomen, lateral (based on *Plectrocnemia australica*); F, fore leg; G, mid leg; H, hind leg. [A. Neboiss, R. Plant]

**Thorax.** The 3 thoracic segments are distinct and well developed (Fig. 40.2A); the pro- and mesonota frequently bear characteristic setal warts, scutum may have a pair of longitudinal bands of setiferous punctures in place of warts; scutellum either with a large median wart or a pair of smaller, elongate warts. Legs slender (Figs 40.2F–H), strongly built, with 5 tarsal segments and a pair of simple terminal claws; coxae long; femora sometimes with a row of setae or stout bristles on outer surface; tibiae with or without long spines or sometimes with fringe of long hair (male *Anisocentropus*); mid legs sometimes dilated in females (*Agapetus*); the apical and preapical socketed spurs are used as diagnostic characters and are expressed as a formula, e.g. 0:2:4 indicates absence of spurs on fore leg, 2 apical spurs on mid leg and 2 apical and 2 preapical spurs on hind leg.

Two pairs of subequal wings (Fig. 40.2B), rarely reduced (some Chathamidae, but not reduced in Australian species), folded roof-like or flat over body when at rest. Wings may be densely covered with fine

hairs (Fig. 40.3A), these sometimes erect and arranged along veins (Fig. 40.3B) or grouped in tufts (*Hydrobiosidae*), some hairs may be modified to scales (*Huxley* and *Barnard* 1988) covering portion of wing (e.g. some *Oecetis* males) (Figs 40.3C, D) or following main veins (*Caenota* males) (Figs 40.3E, F); coarse setae on ventral side of wing assist in wing coupling (*Cheumatopsyche*) (Fig. 40.3J); in some taxa wings almost bare (*Macronematinae*). Venation usually simple and complete, but may be reduced and sexually dimorphic, modifications usually occur in males and may include folds or grooves of wing membrane associated with specialised hairs (Figs 40.3G, H); pterostigma not clearly developed, but indicated by a granular thickening; apical forks formed by branches of major veins; cross-veins few; a corneous spot (nygma) usually present at the base of fork 2, but if that is absent, the spot is located between  $R_{4+5}$  and M. A similar spot is in the fore wing thyridial cell. In fore wing, anal veins looped into each other, so that only one vein reaches the wing margin.

Fig. 40.1 Adult caddis-flies in dorsal view: A, *Ethochorema brunneum*, Hydrobiosidae; B, *Stenopsychodes aureonigra*, Stenopsychidae; C, *Asmicridea edwardsi*, Hydropsychidae; D, *Archaeophylax ochreus*, Limnephilidae; E, *Plectrotarsus gravenhorstii*, Plectrotarsidae; F, *Tascuna ignota*, Oeconesidae; G, *Taskiria austera*, Kokiriidae; H, *Anisocentropus banghaasi*, Calamoceratidae; I, *Triplectides similis*, Leptoceridae. Scales = 4 mm. [J. Green]

The position and arrangement of veins and apical forks are important for identification. The arculus is the point on the postcostal margin of the fore wing where the cubital vein (Cu), sometimes joined by the anal vein (A) runs into the wing margin, and is often surrounded by a small hyaline area. The line of cross-veins between the pterostigma and arculus is known as the anastomosis. The shape and position of hyaline areas in the fore wing is of some diagnostic value at the family level.

Wing coupling is achieved in two basic ways with a number of variations in each. In one arrangement, a jugal lobe on the basal angle of the fore wing links with macrotrichia along the base of the costa of the hind wing (Hydrobiosidae, Philopotamidae and others). In the other, a row of curved macrotrichia, minute hooks or hamuli on the costa of the hind wing curves upwards, and engages with a ventral longitudinal ridge behind the anal veins of the fore wing. In Leptoceridae and Calamoceratidae a short row of spine-like macrotrichia is situated on the upper surface of the hind wing along Sc about midway or towards the distal end of the vein. The second arrangement occurs in the stronger fliers.

Abdominal segmentation is distinct (Figs 40.2D, E), typically comprising 10 segments. The first segment is developed as tergum only; subsequent segments ring-shaped, with tergum and sternum connected laterally by a membranous pleural region; sometimes remnants of tracheal gills are still present; individual segments may be differently sclerotised, covered with hairs or spines, or sculptured (*Helicopsyche*). Segment 5 may have slender lateral filaments (Hydrobiosidae, Polycentropodidae and some Hydropsychidae) or a blunt, elevated protuberance (*Agapetus*). Mesoventral processes may be present on S6–8. Paired internal reticulated sacs are present within segments 6 and 7 of some male Hydropsychidae (Australian *Diplectrona* and *Asmicridea*).

The abdominal segment 8 in males divides into tergum and sternum, but segment 9 forms an annulus (Fig. 40.2D); segment 10 is usually strongly modified; various projections arising from the last segments are diverse in form and constitute the outer genitalic armature. These are generally very useful aids to identification. Neboiss (1986a) illustrates the genitalia of all known Australian species.

In females the genital opening is situated either between S8 and S9 or between S9 and S10. The abdomen (Fig. 40.2E) terminates with one to three pairs of finger-like processes, the middle pair of which probably correspond to cerci (A. Nielsen 1980). Segment 8 is included in the genital region; the shape differs between families. Segment 9 is either divided into tergum and sternum or annular. The terminal segments may be modified to form an ovipositor (*Psyllobetina*, *Ecnomina*, *Philanisia*).

**Internal anatomy.** Alimentary canal relatively short; stomach rather small; intestine tubular, slightly coiled, ending with widened rectal chamber; anus sometimes very distinct, sometimes obscure; 6 Malpighian tubules. Many forms with pair of small glands of uncertain function in abdominal segment 5 of both sexes; these glands often associated with external filaments (Hydrobiosidae, Hydropsychidae). Paired, internal reticulate, membranous sacs (organs) (Mosely and Kimmins 1953) in abdominal segments 6 and 7 of males open posteriorly in pleural areas following these segments (*Smicrophylax*, *Diplectrona*) (Neboiss 1977); the function of these sacs is not known. Nervous system consists of usual cephalic centres, 3 thoracic and 7 abdominal ganglia; 3rd thoracic and 1st abdominal ganglia fused (Glasgow 1936). Testes in form of simple ovoid sacs; proximal part of phallus usually situated within phallocrypt; proximal section of phallocrypt wall and phallus fused to form tubular, phallic apodeme (A. Nielsen 1957). Ovaries consist of numerous, polytrophic ovarioles (Stitz 1904). Colleterial glands paired, usually with either simple or branched accessory lobes (Gower 1967). Muscular studies are usually associated with structure and function of the genital segments (A. Nielsen 1957, 1980).

### Immature Stages

**Egg.** Eggs are spherical or elongate-elliptical, usually with a thin, colourless chorion. They are embedded in a gelatinous matrix known as spumaline, secreted by colleterial glands; this matrix swells as it absorbs moisture. A thin layer of cement-like substance, secreted by the colleterial glands, surrounds the spumaline and adheres to the substrate (Hinton 1981).

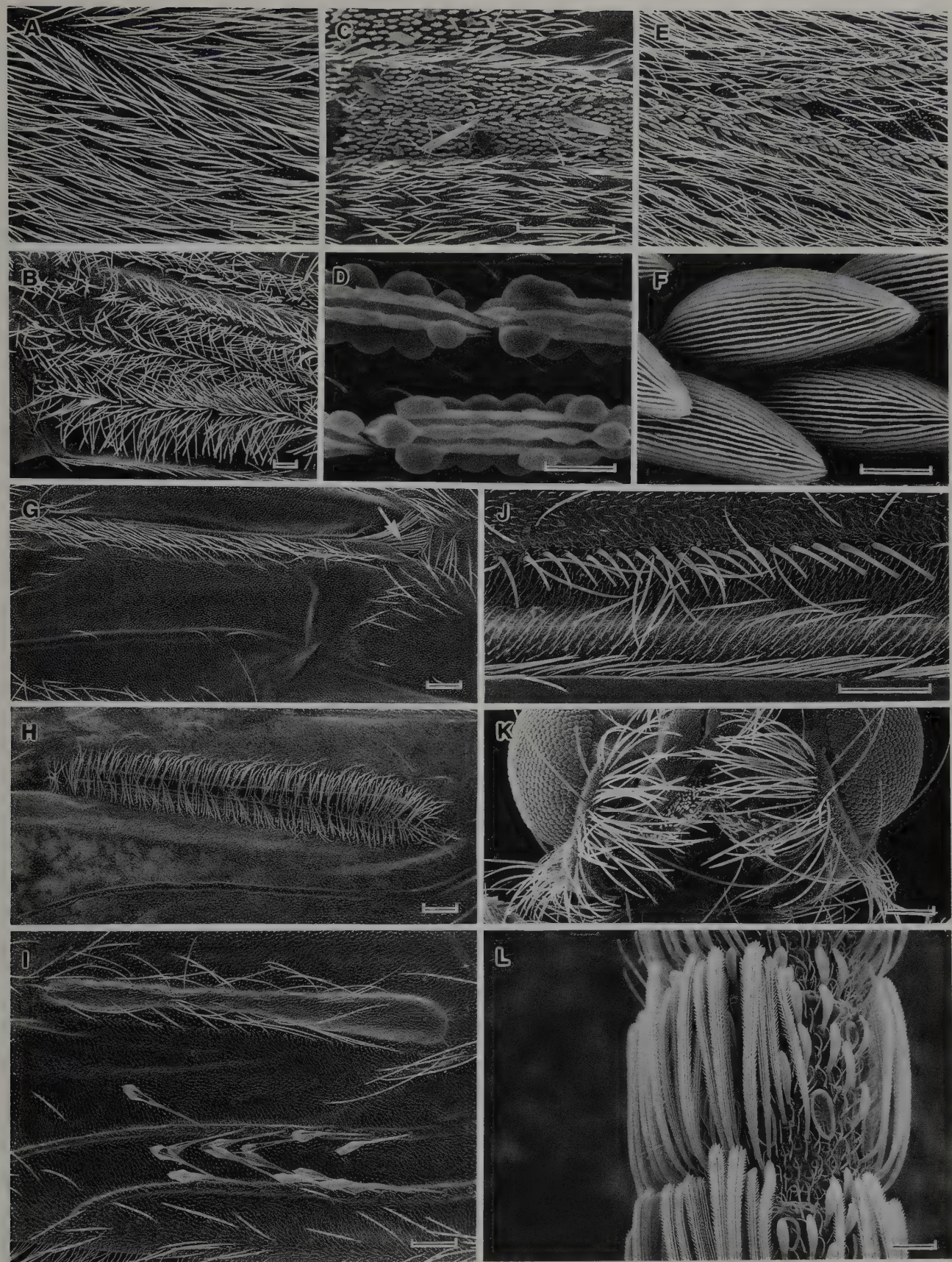
**Larva** (Fig. 40.4G). Head and pronotum always heavily sclerotised, mesonotum sometimes membranous, with small sclerites or entire plate subdivided by median ecdysial line; metanotum membranous, or with sclerites smaller than on mesonotum. Abdomen almost entirely membranous and pale. In dorsal view the head capsule (Fig. 40.4A) consists of 2 parietal sclerites on each side of the head and a frontoclypeal apotome dorsomesally. The Y-shaped ecdysial line separating the frontoclypeal apotome from parietals is known as the frontoclypeal suture, and the section separating both parietals as coronal suture; ventrally (Fig. 40.4B) the parietals may meet at the ecdysial line from the occipital foramen to the submentum, or they may be partly or completely separated by a ventral apotome.

Antennae small, peg-like, clearly visible in some families, rather obscure in others; eyes are comprised of groups of 7 or fewer stemmata; mandibles with cutting edge as a series of pointed teeth or as an entire scraper-like blade, corresponding with the method of feeding;

Fig. 40.3 Details of wing and head: A, *Asmicridea edwardsi*, Hydrobiosychidae, fore wing, dorsal vestiture; B, *Taschorema evansi*, Hydrobiosidae, fore wing, dorsal vestiture; C, *Oecetis pechana*, Leptoceridae, ♂ fore wing, dorsal vestiture, showing section of scale cover; D, same, scales, detail; E, *Caenota plicata*, Calocidae, ♂ fore wing, dorsal vestiture, scales on main veins; F, same, scales, detail; G, *Apsilochorema gisbum*, Hydrobiosidae, ♂ fore wing, ventral, showing discoidal cell fold with pencil of long sensory hairs (arrowed); H, *Taschorema evansi*, Hydrobiosidae, ♂ hind wing, ventral, showing cell-like structure; I, same cell-like structure and androconia on veins A<sub>2</sub> and A<sub>3</sub>, dorsal; J, *Cheumatopsyche modica*, Hydrobiosychidae, fore wing, ventral, with row of coarse setae along central section of vein A<sub>1+2+3</sub>; K, *Caloca straminea*, Calocidae, ♂ head, dorsal, showing mesal depression with sensory hairs; L, *Helyethira simplex*, Hydroptilidae, ♂ antenna, flagellar segments showing whorled, fimbriate hairs and cuticular features. Scales are: A, E, G–L = 100 µm; B, D = 25 µm; C = 300 µm; F = 10 µm.

[K. Pickerd, E. S. Nielsen and A. Wells]







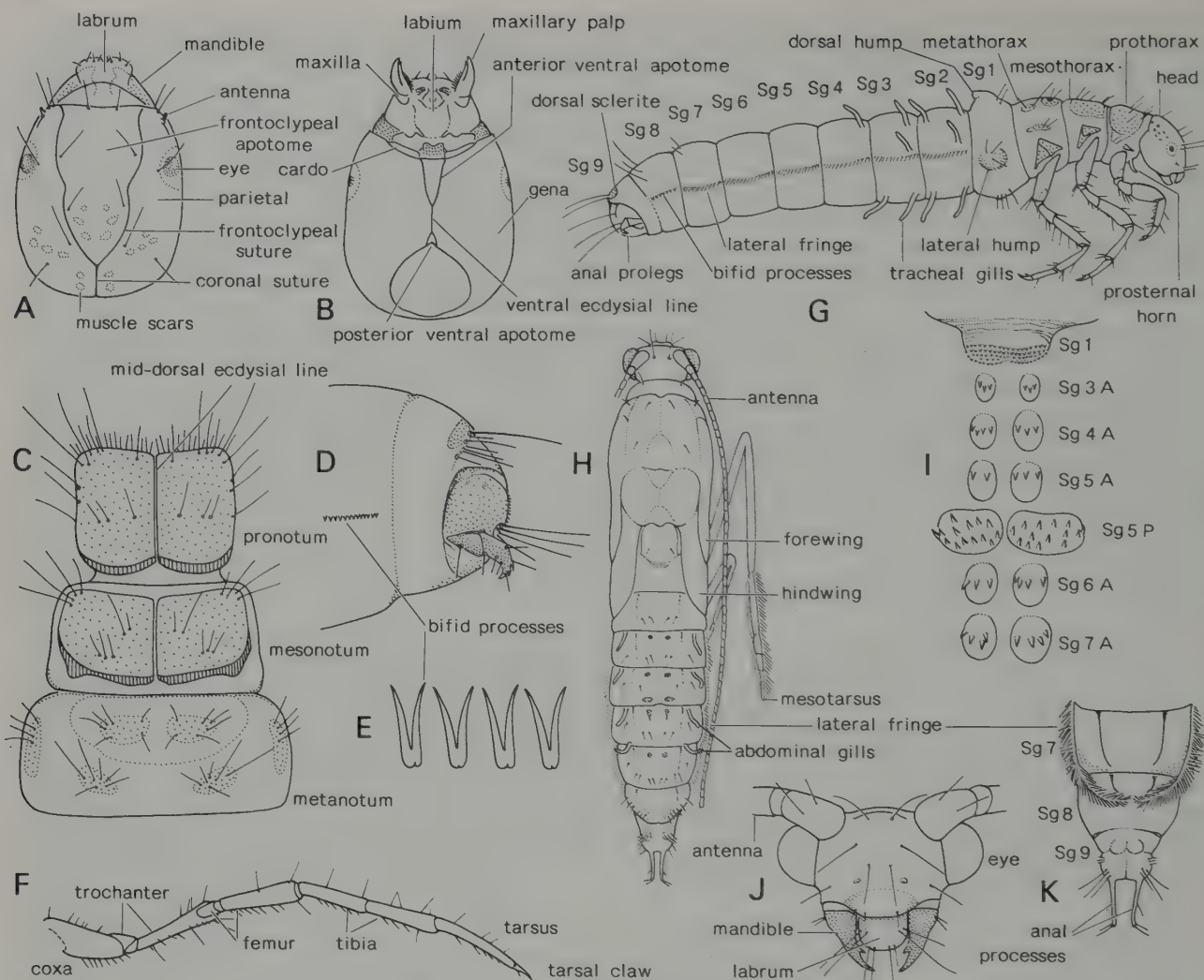


Fig. 40.4 Generalised larva and pupa: A, larval head, dorsal; B, head, ventral; C, thoracic segments, dorsal; D, last abdominal segments, lateral; E, bifid processes of segment 8, enlarged; F, hind leg of a triplectidine leptocerid, showing divided trochanter, femur and tibia; G, larva, lateral; H, pupa, dorsal; I, pupal hook-plates; J, pupal head, frontal view; K, pupa, end segments of abdomen, ventral. [R. Plant]

Sg, segment; Sg....A, Sg....P, anterior and posterior hook-plates.

silk is extruded through a small opening at the tip of the labium.

The 3 thoracic segments are distinct (Fig. 40.4C); pronotum always covered by sclerotised plate, bisected by mid-dorsal ecdysial line; prothoracic pleuron sometimes with distinct trochantin (Figs 40.12 O, P); prosternum frequently with small sclerites; in certain case-making families there is a finger-like membranous prosternal horn (Limnephilidae, Plectrotarsidae). Mesonotum may have sclerotised plates or small sclerites or may be entirely membranous; mesonotal setae arise in 3 primary areas. Metanotum usually membranous, generally with setae grouped on sclerites. The arrangement of sclerites and setae provides diagnostic characters.

Legs 5-segmented, may be armed with spines, combs or setae; fore legs generally shortest; mid and hind tibiae and femora may be secondarily divided into 2 parts (some Leptoceridae) (Fig. 40.4F); the mid tibiae and tarsi are fused in some groups (Philorheithridae); a basal seta on tarsal claw.

The abdomen consists of 9 membranous segments, except for a dorsomedian sclerite on segment 9 in some families. Larvae of most tube-case making families bear a more or less distinct median dorsal hump and paired lateral humps on segment 1; the humps are retractile and may be indistinct in preserved specimens. Larvae of many families have tracheal gills on most abdominal segments; in some families they occur on thoracic segments. Tracheal gills are filamentous extensions of the body wall and may be single or branched, arranged horizontally in dorsal, lateral and ventral rows on each side of abdomen.

The abdomen terminates with a pair of anal prolegs (Fig. 40.4D), which are short and thick, usually armed with a stout accessory hook in case-making larvae (Limnephiloidea), but elongate, separate and very mobile in net-spinning and predatory larvae (Rhyacophiloidea and Hydropsychoidea). In addition, from the margins of the anal opening in some families (Glossosomatidae, Philopotamidae), arise retractile elongate lobes known as anal papillae. In many genera, particularly in



Limnephiloidea, abdominal segments have a lateral fringe of fine filaments. A row of tiny forked lateral tubercles (Figs 40.4D, E), also described as a comb of spicules or bifid processes, may be present on each side of segment 8 (on most abdominal segments in Limnephilidae); these rows are absent from the Tasimiidae, Kokiriidae, Plectrotarsidae and Oeconesidae.

**Pupa** (Fig. 40.4H). Similar to adult except for heavily sclerotised mandibles (Fig. 40.4I), compacted wings, hair fringes on mid tarsi, a lateral fringe of fine filaments and hook-bearing dorsal sclerotised plates (Fig. 40.4I) on the abdomen and a pair of anal processes (Fig. 40.4K).

### Biology

**Reproduction.** Caddis-fly females may deposit their eggs on objects protruding from water, on overhanging vegetation or on ground nearby, or they may simply scatter them over the water surface. Some females actually enter the water and oviposit on specific sites. Eggs are laid singly, in strings or masses of various shapes—spherical, doughnut-shaped or in a coil containing between 20 and several hundred eggs; a maximum of about 800 has been found in *Hydropsyche* (A. Nielsen 1942). Under normal conditions eggs hatch within 3–25 days; little is known of egg diapause in Australian Trichoptera. Caddis-flies are oviparous, with the exception of five Australian species of the genus *Triplectides* which are known to be ovoviviparous (Morse and Neboiss 1982). Terrestrial oviposition has been recorded for two leptocerid species (Towns 1983b); females of the marine species *Philanisus plebeius* deposit their eggs through the papular pores into the coelomic cavity of the small intertidal starfish *Patiriella exigua* (Winterbourn and Anderson 1980).

**Silk Production, Case Construction.** The ability of caddis-fly larvae to produce silk originated in the common ancestor of the sister groups, Trichoptera and Lepidoptera (Wiggins and Mackay 1978), but has evolved differently in each order. Trichoptera larvae are almost entirely aquatic and use silk to construct a variety of nets, shelters or portable cases (Fig. 40.15). These silk constructions allow the larvae to exploit a diverse range of habitats and food resources. Fixed retreats, capture nets and portable cases constructed by larvae vary widely in function, design and materials over the families, but in general, form and function are consistent at the generic level.

Five basic, functional groups of caddis-fly larvae have been recognised according to the pattern of silk utilisation (H. H. Ross 1944; Wiggins 1984b; Mackay and Wiggins 1979): (1) The first group, with simplest usage, are the free-living larvae of Hydrobiosidae and the non-Australian Rhyacophilidae which use silk thread as an anchoring line to allow freedom of movement in strong currents; larvae construct pupal shelters. (2) The larvae of Hydroptilidae are very small and constitute the second group. They are free living in the first (usually four) instars; only in the final (fifth) instar they spin portable, purse-shaped cases from silk, sometimes incorporating sand, diatoms and algae. (3) The saddle-case makers (Glossosomatidae) construct portable cases of small stones with a dome-shaped, dorsal portion and a flat, ven-

tral portion. (4) The functional group known as net spinners or retreat makers, comprises almost entirely the larvae of Hydropsychoidea. They construct fixed shelters or retreats of silk and debris and capture food particles either from current by the aid of specially constructed, silk nets or directly from the substrate. Nearly all are confined to running water. (5) The fifth functional group, known as tube-case makers, comprises most Limnephiloidea. In this group silk is used to construct portable tube-cases of organic or mineral particles. The group also includes Helicopsychidae which make helical snail-like sand cases.

Several conflicting ideas have been advanced regarding the habitats of the ancestral forms. H. H. Ross (1956) concluded from morphological evidence in extant families represented in both lotic and lentic waters, that genera with ancestral character states occur in cool, lotic-erosional habitats, while those with derived character states are in warm, lentic waters. He postulated that larvae of ancestral Trichoptera living in cool running waters lost their spiracles and became wholly dependent on aquatic habitats. They were probably agile, slender, predatory and with simple thoracic legs, much like present day Polycentropodidae. From a study on evolution of feeding tactics and case- or retreat-making behaviour in Trichoptera Weaver and Morse (1986) concluded that neither the free-living nor net-spinning caddis-fly larva was part of the Trichoptera groundplan as suggested by H. H. Ross (1956). They postulated that the ancestral caddis-fly larva most likely was a detritivore tube-case maker, probably inhabiting cold, humus rich, depositional habitats of lentic or lotic waters.

**Larval Habitats.** The transition from lotic to lentic habitats is generally characterised by decreasing elevation, currents and dissolved oxygen, and by less complex substrates, smaller average particle size and increasing water temperatures. In Australia distribution of habitat types is strongly influenced by the rainfall pattern. Lotic systems are found mainly along the eastern and south-eastern mountainous regions, which have a correspondingly greater species diversity (Neboiss 1981). Systems with slower, warmer, less oxygenated water, and bottoms of loose sand and silt, are poorer in species diversity and tend to be found close to the coast, or well inland. Substrates made up of small to medium-sized particles provide a variety of habitats for larvae living on rock surfaces, between or under rocks, in the plant component or periphyton (Bayly and Williams 1973) and within the hyporheic zone (D. D. Williams and Hynes 1974) of the stream. Peripheral areas of sand and silt with plant debris provide habitats for larvae, as do submerged, water-soaked pieces of wood, roots of terrestrial plants extending into the water, and stems and leaves of aquatic plants. Special habitat conditions are found in springs, spring-fed seepage pools, waterfall splash zones or on rock-face seepages. In marked contrast are large rivers, swamps, marshlands, ponds, lakes, reservoirs, farm dams, temporary pools and saline rivers or lakes. Many of these habitats are occupied by only restricted representatives of genera or families.



There is now a considerable amount of evidence that demonstrates the sensitivity of Trichoptera larvae to various water pollutants. The effects of pollution on aquatic organisms have been investigated in some detail by Resh and Unzicker (1975), Resh (1979) and many other authors who discuss the use of indicator organisms, as well as community diversity, in evaluating water quality. Trichoptera larvae rate high amongst these organisms.

**Feeding.** Adult Trichoptera have reduced mouth-parts and normally do not feed, although some may occasionally imbibe water or nectar. The larval stage occupies most of the life cycle and is the main feeding period. Feeding ceases once the larva reaches maturity and seals itself inside the pupal chamber. According to the type of feeding, larvae have been grouped into four (Wiggins 1977) or five (Unzicker *et al.* 1982) categories:

1. *Shredders-chewers*: herbivores feeding on live vascular plants and filamentous algae, or detritivores consuming decomposing vascular plant tissue. (Some Hydroptilidae, Leptoceridae, Polycentropodidae and Calamoceratidae.)

2. *Collectors*: filter or suspension feeders and gatherers feeding on fine organic particles. (Certain genera of Hydroptilidae, Philopotamidae, Glossosomatidae and some species of Leptoceridae.)

3. *Scrapers*: herbivores, grazing scrapers, feeding upon periphyton and fine organic particles. (Glossosomatidae, Helicopsychidae, some Hydroptilidae and Leptoceridae.)

4. *Piercers*: herbivores sucking fluids from living plant tissues. (Some Hydroptilidae.)

5. *Predators*: swallows or engulfers, carnivores feeding on whole animals, parts of animals, or fish or insect eggs. (Hydrobiosidae, Hydropsychidae, some Hydroptilidae, Leptoceridae and Polycentropodidae.)

Some families are represented in more than one of these categories as different genera are adapted to different feeding methods. Larval diets may change from early to late instars, or from season to season determined by availability of certain food, or may be affected by physical factors like stream current, water depth, substrate type, temperature or geographic situation. In general terms the net-spinners (Hydropsychidae, Philopotamidae, Polycentropodidae) are collectors and gatherers; the case-makers (Hydroptilidae, Calamoceratidae, Leptoceridae and others) are shredders, chewers, grazers, scrapers and piercers, and the free-living forms (Hydrobiosidae) are predators.

**Pupation.** The mature larva usually moves to a sheltered place in the stream and modifies the larval case or constructs a special pupal shelter prior to metamorphosis. The period during which the larva stops eating, seals itself in the case and rests before ecdysis is termed the prepupal period (Wiggins 1977).

Mature larvae of Hydrobiosidae and Glossosomatidae spin closely-woven silken cocoons inside the pupal shelter. Species in the superfamily Hydropsychoidea convert part of their retreat to a pupal chamber, while case-makers often shorten their cases before sealing each end with a perforated silken cap—the pupa lies free within the old larval case.

The pupal period ends when the pupal integument becomes separated from the enclosed adult. With the aid of strong mandibles and the hook-bearing abdominal plates, the pharate adult leaves the case and swims to the surface by means of fringed tarsi on the middle legs. The final moult usually occurs above the water surface on some emergent plant or other object. The pupal period usually lasts 15–25 days. Emergence times may vary from season to season. Once the adult has emerged from the pupal skin its wings expand to full size and harden before flight.

**Natural Enemies.** Caddis-fly larvae and adults are preyed upon by other insects and their larvae (Coleoptera, Megaloptera, Plecoptera). Hymenoptera parasitise larvae and pupae in Europe and Asia but have not been recorded from Australia; however, there are records of Chironomidae attacking larvae, and water mites (Hydracarina) parasitising larvae and adults. Nematomorpha (gordian worms) have been found inside the bodies of adults. On some occasions more than half of the captured specimens have been parasitised (e.g. *Conoesucus norelus*, Conoesucidae, at a Tasmanian locality in 1972). An unidentified triungulin has been found attached to the maxillary palp of a male *Agapetus* sp. collected at Mitta Mitta R., Vic.; there are, however, no records of Strepsiptera from Trichoptera.

**Economic Importance.** Caddis-flies constitute a significant portion of the food chain in freshwater ecosystems. The larvae feed on plant and animal tissue and have been recorded causing minor damage to submerged wooden structures and natural fibre nets (Malicky 1973). More serious, however, is damage to aquatic plants (e.g. water lilies) in commercial and ornamental pools, where larvae of some species of Triplectidinae (Leptoceridae) chew off stems of leaves and flowers; leptocerid larvae have been recorded damaging young rice plants in paddy fields. Mass occurrences of net-spinning hydropsychid larvae can cause fouling of water, or their presence on the walls of water channels and pipes leading to power houses can restrict water flow to such a degree that power production is affected. Adults, when attracted to light in enormous numbers can reduce visibility thus affecting traffic flow, spoiling freshly painted surfaces and occasionally causing allergic reactions in humans.

The usefulness of caddis-flies outweighs their deleterious effects. They constitute a major part of the diet of trout which swallow case and contents entire. The adults are taken by birds, bats, amphibians and reptiles. The importance of caddis-flies as water quality indicators has already been noted.

### Special Features of the Australian Fauna

Wiggins (1984a) surmises that diversification at family level in Rhyacophiloidea and Hydropsychoidea preceded separation of Laurasia and Gondwana, as almost all families in these two superfamilies are represented on modern fragments of both supercontinents. In contrast, divergence within the case-building Limnephiloidea can be attributed to breakup of Pangaea as, with few exceptions, the fami-



lies are endemic to land masses of either Laurasian or Gondwanan origin.

The world fauna is divided into 43 families, of which 25 families, representing all three superfamilies, are recognised in the Australian fauna (Neboiss 1986a). The number of species recognised in Australia is rapidly increasing and at the beginning of 1990 stood at 478. This number includes some undescribed species. Preliminary work on several genera indicates considerable additional new species, but it is too early to present an estimate. Unavoidably this work will change the proportional family representation, but at present the highest number of species (101) is known from Hydroptilidae, constituting about 21% of the Australian Trichoptera fauna; Leptoceridae—83 species (17%), Ecnomidae—57 species (12%) and Hydrobiosidae—57 species (12%). Of the remaining 21 families, 14 represent between 1 and 5% each, and 7 families are below 1% each.

The Australian caddis-fly fauna has close affinities with the families and genera in New Zealand and South America. However, most species are endemic to Australia. A high proportion of endemism is also recorded from small, geographically isolated areas like Tas. with 74% endemic species (Neboiss 1977) and south-

western Australia 79% (Neboiss 1982). The northern Australian fauna shows strong Oriental and Papuan influences. It is dominated by Leptoceridae, particularly the genera *Oecetis* and *Triaenodes* (Neboiss 1981). Of the other families, Hydroptilidae, with 101 species, is the largest in Australia and besides the endemic component has affinities with New Zealand and Papuan regions.

Two endemic families occur in Australia—Plectrotarsidae and Antipodoeciidae although the latter may be only a branch of Conoesucidae. Four families—Conoesucidae, Calocidae, Oeconesidae and Chathamidae—are shared with New Zealand, but the Australian-South American connections over Antarctica are demonstrated in the distribution of Helicophidae, Kokiriidae, Tasimiidae and Philorheithridae. The single Australian limnephilid genus, *Archaeophylax*, belongs to the primitive subfamily Dicosmoecinae, which also includes certain South American genera (Wiggins 1984a). An unusual distribution is recorded for the family Atriplectididae, which occurs in southern Australia and the Seychelles Is. The Chathamidae is the only family with marine larvae and is found in water of normal oceanic salinity, in the intertidal zone of rocky sections of N.S.W. It also occurs in New Zealand and on the Chatham and Kermadec Is.

## CLASSIFICATION

### Order TRICHOPTERA (478 Australian species)

#### RHYACOPHILOIDEA (168)

- Rhyacophilidae (0)
- 1. Hydrobiosidae (57)
- 2. Glossosomatidae (10)
- 3. Hydroptilidae (101)

#### HYDROPSYCHOIDEA (126)

- 4. Philopotamidae (19)
- 5. Stenopsychidae (9)
- 6. Hydropsychidae (27)
- Arctopsychidae (0)
- 7. Polycentropodidae (12)
- Dipseudopsidae (0)
- 8. Ecnomidae (57)
- 9. Psychomyiidae (2)
- Xiphocentronidae (0)

#### LIMNNEPHILOIDEA (184)

- Phryganeidae (0)
- Phryganopsychidae (0)
- Brachycentridae (0)
- 10. Limnephilidae (3)
- 11. Plectrotarsidae (5)
- 12. Oeconesidae (1)
- Goeridae (0)
- Uenoidae (0)
- Lepidostomatidae (0)
- 13. Tasimiidae (6)
- 14. Chathamidae (1)
- Anomalopsychidae (0)
- Beraeidae (0)
- Sericostomatidae (0)
- 15. Conoesucidae (21)

- 16. Antipodoeciidae (1)
- 17. Helicopsychidae (6)
- Barbarochthonidae (0)
- Hydrosalpingidae (0)
- Petrothrincidae (0)
- 18. Calocidae (18)
- 19. Helicophidae (6)
- Limnocentropodidae (0)
- 20. Kokiriidae (5)
- 21. Philorheithridae (13)
- 22. Odontoceridae (4)
- 23. Atriplectididae (1)
- Molannidae (0)
- 24. Calamoceratidae (10)
- 25. Leptoceridae (83)

The once widely accepted subdivision of Trichoptera into two suborders Annulipalpia and Integripalpia (Martynov 1924), is no longer used. In its place, H. H. Ross's phylogenetic separation into three superfamilies is now more widely accepted (Ross 1956, 1967; Malicky 1973; Wiggins 1977, 1982, 1987). Schmid (1980) considered the superfamily Rhyacophiloidea as monophyletic and included it, together with Hydropsychoidea, in the

Annulipalpia, while Integripalpia was also split into two superfamilies, Limnephiloidea and Leptoceroidea. A new classification of the subordinal taxa was proposed by Weaver (1984) and Weaver and Morse (1986), but its effectiveness is yet to be verified. The classification adopted here, with some modifications and amendments, follows that used by Wiggins (1982).

### Key to the Families of Trichoptera Known in Australia

#### ADULTS

1. Insects small, usually 5 mm or less in length; antennae shorter than fore wing; maxillary palps 5-segmented in both sexes; scutellum flat, triangular, pointed posteriorly, margins vertical (Fig. 40.5c); mesoscutum without setal warts; wings narrow, pointed apically (Fig. 40.7d), fringes very long, those of hind wing usually longer than width of the wing ..... **Hydroptilidae** (p. 800)

Insects usually more than 5 mm long; antennal length variable, up to 3 times the length of fore wing; maxillary palps 1–6 segmented in ♂♂, 5- or 6-segmented in ♀♀; scutellum broad posteriorly, convex, without vertical margins (Fig. 40.5B); mesoscutum frequently with setal warts; wings broad, fringes usually short, less than width of wing .....		2
2(1).	Ocelli present (Fig. 40.5A) .....	3
	Ocelli absent (Fig. 40.5F) .....	7
3(2).	Maxillary palps with segment 5 flexible or annulate, distinctly longer than segment 4 (Fig. 40.7I) .....	Philopotamidae (p. 801)
	Maxillary palps 3- or 5-segmented, apical segment not flexible or annulate, about same length or shorter than preceding segment .....	4
4(3).	Maxillary palps 5-segmented in both sexes, segments 1 and 2 short, stout; without setal warts on mesoscutum .....	5
	Maxillary palps 3-segmented in ♂♂, 5-segmented in ♀♀; segment 1 short, cylindrical; segment 2 usually longer than segment 1, mesoscutum with setal warts or 2 parallel bands of setose punctures .....	6
5(4).	Segment 2 of maxillary palps with globular, mesally directed, lateral projection (Fig. 40.7G) .....	Glossosomatidae (p. 800)
	Segment 2 of maxillary palps cylindrical, without lateral projection .....	Hydrobiosidae (p. 798)
6(4).	Mesoscutum with one pair of elongate setal warts (Australian species only) (Fig. 40.5L) .....	Limnephilidae (p. 805)
	Mesoscutum with 2 parallel bands of setose punctures mesally and 2 small groups posteriorly, either side of scutellum (Fig. 40.5N) .....	Plectrotarsidae (p. 805)
7(2).	Labial palps absent or vestigial .....	8
	Labial palps present, normal .....	9
8(7).	Maxillary palps vestigial; mouth-parts absent; mesoscutum without setal warts .....	Hydropsychidae (pt, p. 801)
	Maxillary palps reduced, segment 5 short, about as long as segment 4, not annulate; mouth-parts present; mesoscutum with pair of setal warts .....	Polycentropodidae (pt, p. 803)
9(2).	Maxillary palps 5-segmented in both sexes; apical segment flexible, annulate, at least twice as long as segment 4 (Fig. 40.7L) .....	10
	Maxillary palps 1- to 6-segmented in ♂♂, 5- or 6-segmented in ♀♀; apical segment generally short, not flexible, apical one or 2 segments sometimes granular in texture, but not annulate (Fig. 40.10r) .....	14
10(9).	Mesoscutum without setal warts (Figs 40.5F, G) .....	Hydropsychidae (pt, p. 801)
	Mesoscutum with setal warts (Fig. 40.5H) .....	11
11(10).	Fore wing vein R <sub>1</sub> forked at apex (sometimes difficult to see) (Fig. 40.8F) .....	Ecnomidae (p. 803)
	Fore wing vein R <sub>1</sub> not forked at apex .....	12
12(11).	Mesoscutal warts separated by anterior extension of scutellum (Fig. 40.5E) .....	Stenopsychidae (p. 801)
	Mesoscutal warts not separated by anterior scutellar extension (Fig. 40.5H) .....	13
13(12).	Maxillary palps with segment 3 arising before apex of segment 2; fore wing thyridial cell just touches or overlaps base of median cell; tibial spurs 3:4:4 .....	Polycentropodidae (pt, p. 803)
	Maxillary palps with segment 3 arising at apex of segment 2; fore wing thyridial cell very small, usually distinctly separated from base of median cell; tibial spurs 2:4:4 .....	Psychomyiidae (p. 803)
14(9).	Mid tibia with preapical spurs .....	15
	Mid tibia without preapical spurs .....	21
15(14).	Maxillary palp segment 1 short, expanded apicomesally and bearing a tuft of setae (Fig. 40.10E) .....	Philorheithridae (p. 809)
	Maxillary palp segment 1 elongate, without apicomesal expansion .....	16
16(15).	Mesoscutum with one pair of setal warts .....	17
	Mesoscutum without setal warts, but with 2 longitudinal bands or groups of setiferous punctures .....	19
17(15).	In fore and hind wings R <sub>1</sub> joins R <sub>2</sub> before wing margin (Fig. 40.8j); maxillary palps of ♂ 1- or 2-segmented (in <i>Tascuna</i> 1-segmented) .....	Oeconesidae (p. 805)
	In fore and hind wings R <sub>1</sub> reaches wing margin separately from R <sub>2</sub> ; maxillary palps of ♂ 3- or 4-segmented .....	18
18(17).	Head with mouth-parts slightly to considerably extended; fore wing vein R <sub>1</sub> joins Sc basad of pterostigma by short cross-vein or sharp bend; discoidal cell closed (Fig. 40.9A); maxillary palps of ♂ 3-segmented .....	Kokiriidae (p. 809)
	Head with mouth-parts normal, not extended; fore wing vein R <sub>1</sub> without sharp bend, not joined to Sc by cross-vein; discoidal cell open (Fig. 40.8i); maxillary palps of ♂ 4-segmented .....	Tasimiidae (p. 807)
19(16).	Fore wing median cell closed (Fig. 40.10G); maxillary palps 6-segmented in both sexes; spurs 2:4:3 ( <i>Anisocentropus</i> ) .....	Calamoceratidae (p. 813)
	Fore wing median cell open or absent; maxillary palps 5-segmented in both sexes; spurs 2:4:4 .....	20
20(19).	Fore wing veins R <sub>1</sub> and R <sub>2</sub> join shortly before wing margin (Fig. 40.10j) .....	Odontoceridae (p. 813)
	Fore wing veins R <sub>1</sub> and R <sub>2</sub> run separately to wing margin (Fig. 40.10h) .....	Atriplectididae (p. 813)
21(14).	Mesoscutum with one pair of setal warts (Fig. 40.6F), sometimes indistinct .....	22
	Mesoscutum without setal warts, but may have 2 parallel bands of setose punctures .....	23
22(21).	Fore wing rounded apically, discoidal cell closed; scutellum with pair of warts, sometimes fused mesally; at least first few abdominal sternites with reticulate pattern .....	Helicopsychidae (p. 809)
	Fore wing acute apically, discoidal cell open; scutellum with one, mesal, dome-shaped setal wart (Fig. 40.5R); abdominal sterna without reticulate pattern .....	Antipodoeciidae (p. 807)



- 23(21). Mesoscutum without bands of setose punctures; setae, if present, minute and scattered ..... 24  
 Mesoscutum with pair of irregular bands of setose punctures, extending for part or entire length of mesoscutum ..... 26
- 24(23). Wing coupling by hamuli on basal section of costal margin of hind wing, distal hamuli more closely grouped; jugal lobe reduced; hind wing with large, vein-free area discally (Fig. 40.9D) ..... **Helicophidae** (p. 809)  
 Wing coupling by enlarged hairs along costal margin of hind wing, hairs at most only slightly curved; jugal lobe well developed; hind wing discal area without vein-free area (Fig. 40.9E) ..... 25
- 25(24). Pronotum with 2 pairs of setal warts, mesal pair small, rounded, lateral pair oval (Fig. 40.5P) (except ♂ of *Caenota*, where only one elongate pair is present, but then hind wing vein  $R_1$  joins Sc for short distance before ending separately at wing margin (Fig. 40.9I)); fore wing anal vein joins Cu before wing margin ..... **Calocidae** (p. 809)  
 Pronotum with pair of elongate setal warts (Fig. 40.5T); fore wing anal vein terminates at wing margin basad of and separately from Cu (Fig. 40.9E); hind wing vein  $R_1$  usually runs free to wing margin, rarely Sc joins  $R_1$  near margin ..... **Conoesucidae** (p. 807)
- 26(23). Antennae stout, about as long as fore wing (longer in brachypterous species); scutellum with pair of indistinctly fused warts; maxillary palps stout, 5-segmented in both sexes, segment 2 lengthened, produced beyond insertion of segment 3 in ♂ (Fig. 40.8H) ..... **Chathamiidae** (p. 807)  
 Antennae filiform, slender, 2–3 times as long as fore wing; scutellum without warts but may have few setiferous punctures; maxillary palps slender, 5-segmented and similar in both sexes, segment 2 unmodified (Fig. 40.10L) ..... **Leptoceridae** (p. 816)

### LARVAE (by J. C. Dean)

Kokiriidae and Oeconesidae are included in the key on the basis of unidentified larvae agreeing with family descriptions presented by Cowley (1978) based on confirmed New Zealand larvae. Stenopsychidae and Psychomyiidae are omitted; a larva which may belong to the former keys to Polycentropodidae.

1. First abdominal segment of larvae with dorsal and/or lateral protuberances, lateral protuberances usually with small sclerites or a pad-like surface bearing spines, spicules or setae; anal claws lateral on apparent 10th abdominal segment formed by fusion of abdominal prolegs; constructing portable cases ..... Superfamily LIMNEPHILOIDEA. 8  
 First abdominal segment of larvae without protuberances or lateral pad-like surfaces; anal claws terminal on well developed abdominal prolegs (except Hydroptilidae); free living (Hydrobiosidae and early instar Hydroptilidae), living in fixed retreats (Hydropsychoidea) or constructing portable cases (Glossosomatidae and Hydroptilidae) ..... Superfamilies RHYACOPHILOIDEA and HYDROPSYCHOIDEA. 2
- 2(1). Dorsal sclerotisation on first thoracic segment only ..... 3  
 Dorsal sclerotisation on all three thoracic segments, although incomplete on meso- and metanota in some families ... 5
- 3(2). Labrum membranous, anterior margin considerably broader than posterior margin (Fig. 40.11P) ..... **Philopotamidae** (p. 801)  
 Labrum sclerotised, anterior margin not broader than posterior margin ..... 4
- 4(3). Fore trochantin distinct and well developed; fore leg not modified (Fig. 40.12L) ..... **Polycentropodidae** (p. 803)  
 Fore trochantin reduced, not at all obvious; fore leg modified, either chelate (Fig. 40.11F) or with femur broadened and bearing a field of stout spines (Fig. 40.11E) ..... **Hydrobiosidae** (p. 798)
- 5(2). Meso- and metanota each bearing a pair of small sclerites (Fig. 40.11K); constructing dome-shaped portable stone case ..... **Glossosomatidae** (p. 800)  
 Meso- and metanota with sclerotisation complete or almost complete; not constructing stone cases ..... 6
- 6(5). Abdominal gills present (Figs 40.12A, F) ..... **Hydropsychidae** (p. 801)  
 Abdominal gills absent ..... 7
- 7(6). Abdomen of final instar larva swollen, much broader and deeper than head and thorax (Figs 40.11L, M); abdominal prolegs not well developed; final instar larva portable purse-shaped case maker ..... **Hydroptilidae** (p. 800)  
 Abdomen not swollen, only slightly broader and deeper than head and thorax; abdominal prolegs well developed; living in fixed retreats (Fig. 40.12O) ..... **Ecnomidae** (p. 803)
- 8(1). Larva constructing helical case of sand grains (Fig. 40.14L); anal claw with comb-like structure (Fig. 40.14M) ..... **Helicopsychidae** (p. 809)  
 Larva not constructing helical case of sand grains; anal claw with dorsal accessory hook simple or absent ..... 9
- 9(8). Head comparatively small, narrow, without visible ecdysial lines (Fig. 40.14A); pronotum with 2 pairs of sclerites on anterior half, posterior half membranous and retractable into mesonotum ..... **Atriplectididae** (p. 813)  
 Head not reduced, ecdysial lines distinct; pronotum completely sclerotised, not retractable into mesonotum ..... 10
- 10(9). Mid leg with tibia and tarsus fused ..... 11  
 Mid leg with tibia and tarsus not fused ..... 12
- 11(10). Tibia and tarsus fused in fore leg (Figs 40.13F, G); ventral apotome of head capsule extending to occipital foramen, completely separating genae ..... **Kokiriidae** (p. 809)  
 Tibia and tarsus not fused in fore leg (Fig. 40.14I); ventral apotome of head capsule short, not reaching to occipital foramen (Fig. 40.14G) ..... **Philorheithridae** (p. 809)
- 12(10). Prosternum with median horn-shaped process ..... 13  
 Prosternum without median horn-shaped process ..... 14
- 13(12). Venter of 1st abdominal segment with 3 pairs of setae ..... **Plectrotarsidae** (p. 805)

- Venter of 1st abdominal segment with numerous setae ..... **Limnephilidae** (p. 805)
- 14(12). Metasternum with 2 or more setae ..... 15  
Metasternum without setae ..... 16
- 15(14). Femur of hind leg divided into short proximal and longer distal sections (Fig. 40.4F); antennae obvious, relatively long, usually longer than 1/5 the width of anterior margin of frontoclypeal apotome, located close to frontal edge of head capsule (Fig. 40.14v) (except in *Triplexa*, antennae minute, about half way between eye and base of mandible); fresh water, some in brackish waters (*Symphitoneuria*) ..... **Leptoceridae** (p. 816)  
Femur of hind leg not divided into 2 sections; antennae short, less than 1/5 the width of anterior margin of frontoclypeal apotome, located halfway between eyes and frontal edge of head capsule (Fig. 40.12r); marine intertidal ..... **Chathamiidae** (p. 807)
- 16(14). Abdominal segments with lateral fringe of fine filaments ..... 17  
Abdominal segments without lateral fringe ..... 19
- 17(16). Head capsule with prominent carina (Fig. 40.13M) ..... **Oeconesidae** (p. 805)  
Head capsule without carina ..... 18
- 18(17). Eyes bulging, contained in semi-circular dorsal protuberances of the head capsule (Fig. 40.13A); venter of 1st abdominal segment bearing setae; case constructed of small stones ..... **Tasimiidae** (p. 807)  
Eyes not bulging (Fig. 40.14p); venter of 1st abdominal segment without setae; case constructed of 2 ovate pieces of leaf, dorsal piece larger than ventral ..... **Calamoceratidae** (p. 813)
- 19(16). Prosternum with large sclerite(s) ..... **Odontoceridae** (p. 813)  
Prosternum membranous ..... 20
- 20(19). Ventral surface of head capsule with genae widely separated at occipital foramen (Fig. 40.13R) ..... **Conoesucidae** (p. 807)  
Ventral surface of head capsule with genae close together and almost abutting at occipital foramen (Figs 40.13r, x) ..... 21
- 21(20). Strong carina extending obliquely across pronotum, terminating in a pointed and dorsoventrally flattened projection at each anterolateral corner (Fig. 40.13v) ..... **Antipodoeciidae** (p. 807)  
Carina absent or, if present, parallel to lateral margin of pronotum, not terminating in a projection at each anterolateral corner ..... 22
- 22(21). Antennae situated very close to eyes (Fig. 40.13w) ..... **Calocidae** (p. 809)  
Antennae situated about halfway between eyes and frontal edge of head capsule (Fig. 40.14D) ... **Helicophidae** (p. 809)

### Superfamily RHYACOPHILOIDEA

Adults with 5-segmented maxillary palps in both sexes, terminal segment similar in structure to preceding segment, neither annulate nor flexible. Antennae with short, stout basal segment, shorter than head, flagellum does not exceed length of fore wing. Females with single anal-vaginal opening, abdominal segment 10 with pair of cerci.

Larvae mobile, free living or constructing portable cases (Cartwright and Dean 1982); head with antennae not apparent, if present, close to anterior margin of head; well developed sclerites on all thoracic nota or only on pronotum; legs about equal in length; abdomen lacking dorsal and lateral spacing humps on segment 1, and lateral fringe; dorsal sclerite present on segment 9, anal prolegs either free or variously fused.

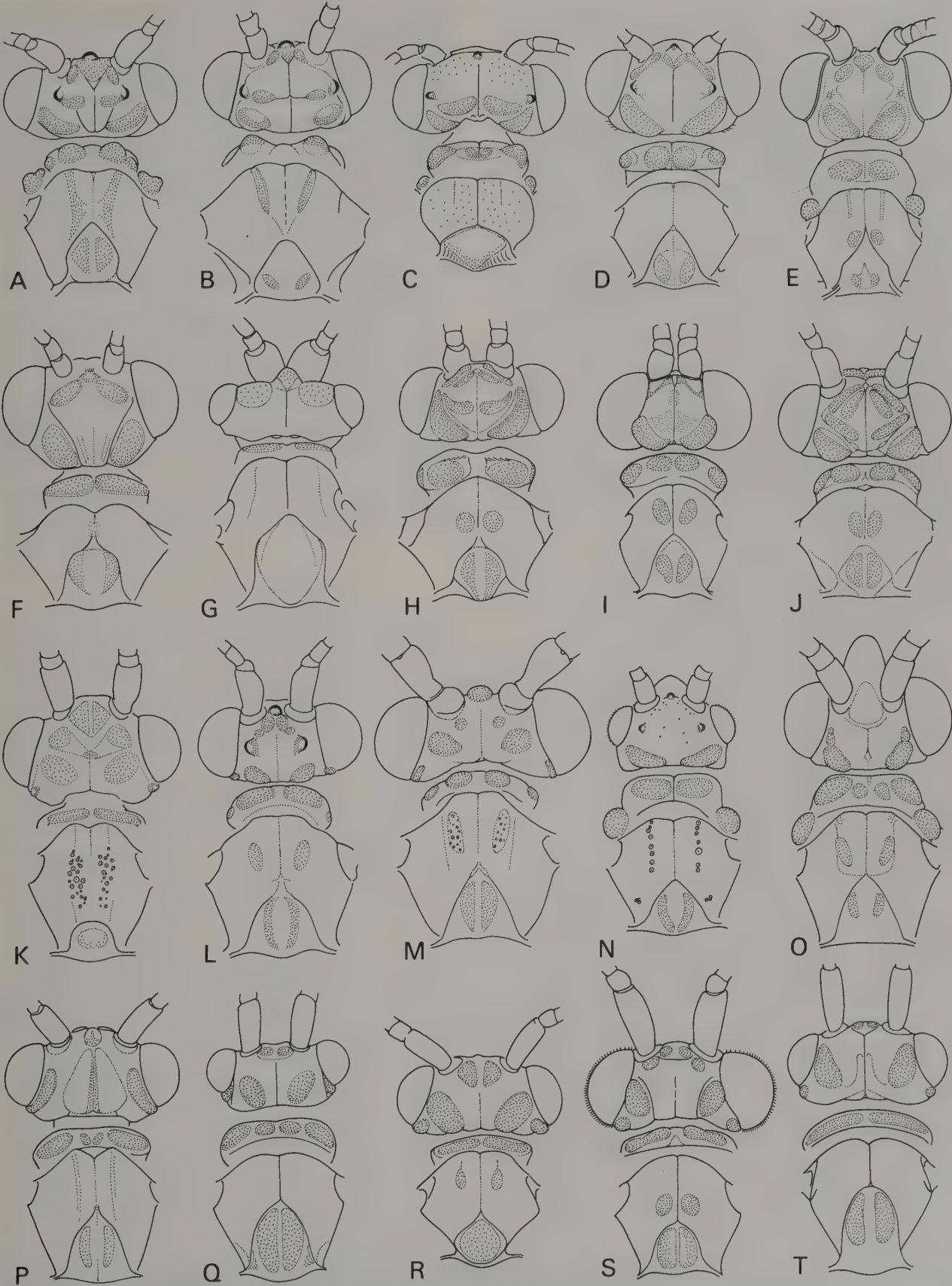
**1. Hydrobiosidae.** Adults medium sized (Fig. 40.1A), with wing span 10–30 mm, wings dark brown to black, often mottled; males usually with small areas of modified setae. Ocelli present. Maxillary palps 5-segmented in both sexes, segments 1 and 2 cylindrical, shorter than others, terminal segment simple; antennae as long as or slightly shorter than fore wing. Mesoscutum and scutellum with-

out setal warts (Fig. 40.5A). Wings elongate, ovate, venation complete, often differing in sexes (Figs 40.7A–C); fore wings with hyaline line along M and hyaline areas around cross-veins *r-m*, *m-cu* and at arculus; vestiture in some genera evenly pubescent, arranged along veins (Fig. 40.3B), or with tufts of thickened upright hairs on veins; discoidal cell closed or open in fore wing, open in hind wing. Lateral filament to S5 in male often present; prominent ventromesal projection generally on abdominal segments 6, 7 or 8. Female abdomen in some genera terminates in slender ovipositor. Tibial spurs 1:4:4 or 2:4:4.

Larvae (Figs 40.11A–F) of Hydrobiosidae are free living, prognathous (Fig. 40.11A) and usually inhabit mainly cool, fast-flowing mountain streams; a few are adapted to slow-flowing waters or even tolerate stagnant pools. They are predatory, mainly on other aquatic insects. The body is smooth with few, scattered, bristle-like hairs, colour varying from pale creamy white to greenish, only head and pronotum sclerotised. Fore legs modified (Figs 40.11E, F); usually chelate or subchelate with tibia and tarsus reduced and claw closing against distal projection of femur. Abdominal gills absent; anal prolegs (Figs 40.11B, C) long and stout, apical segment sclerotised,

Fig. 40.5 Dorsal view of adult head, pro- and mesonota: A, *Ulmerochorema rubiconum*, Hydrobiosidae; B, *Agapetus* sp., Glossosomatidae; C, *Oxyethira columba*, Hydroptilidae; D, *Chimarra uranka*, Philopotamidae; E, *Stenopsychodes mjobergi*, Stenopsychidae; F, *Asmicridea edwardsi*, Hydropsychidae-Hydropsychinae; G, *Baliomorpha banksi*, Hydropsychidae-Macronematinae; H, *Plectrocnemia australica*, Polycentropodidae-Polycentropodinae; I, *Hyalopsyche disjuncta*, Polycentropodidae-Hyalopsychinae; J, *Ecnomus tillyardi*, Ecnomidae; K, *Philanisus plebeius*, Chathamiidae; L, *Archaeophylax ochreus*, Limnephilidae; M, *Tascuna ignota*, Oeconesidae; N, *Plectrotarsus gravenhorstii*, Plectrotarsidae; O, *Tanjistomella verna*, Kokiriidae; P, *Caloca ascita*, Calocidae, ♂; Q, *Caenota plicata*, Calocidae, ♀; R, *Antipodoecia turneri*, Antipodoeciidae; S, *Tasiagma ciliata*, Tasimiidae; T, *Lingora* sp., Conoesucidae. [R. Plant, A. Neboiss]





claws simple. Larva constructs crude pupal chamber of small stones; pupa enclosed within amber-coloured, silken cocoon.

The family occurs predominantly in the Australasian and Neotropical regions, although a few species are found in the Oriental, Nearctic and Palaearctic regions. Until recently this group was regarded as a subfamily within the family Rhyacophilidae. There are about 40 genera with approximately 150 species, placed in two subfamilies—*APSILOCHOREMINAE* and *HYDROBIOSINAE*. Both subfamilies, with 14 genera and 57 species, are known from Australia.

**2. Glossosomatidae.** Adults small, dull, greyish to black, with wing span 8–12 mm; all rather uniform in appearance. Ocelli present. Maxillary palps (Fig. 40.7G) 5-segmented in both sexes; first 2 segments short, subequal, 2nd with globular mesolateral projection, 3rd segment the longest. Antennae stout, shorter than fore wing.

Mesoscutum and scutellum each with pair of setal warts (Fig. 40.5B). Fore wings elongate, ovate, discoidal cell closed (Fig. 40.7F). Dorsal margin of S5 in both sexes with small, lateral, blister-like protuberance. In females mid tibia and tarsus more or less dilated (Fig. 40.7E), abdominal segments 8 and 9 each with long internal

apodeme on either side; abdomen terminates with pair of slender, 2-segmented cerci. Tibial spurs 2:4:4.

Larvae (Figs 40.11H–K) inhabit cool, fast-flowing streams; feed on algae and fine organic particles. They are usually referred to as saddle-case makers and construct dome-shaped cases of small stones; the ventral side of the case is flattened and made of smaller grains (Fig. 40.11H). Abdominal gills and lateral fringe absent; anal papillae present (Fig. 40.11i); anal claws with one or 2 accessory hooks. Shortly before pupation the larva removes the flattened ventral part of the case and fastens the upper section to the substrate. The pupa is enclosed within a greyish or brownish silk cocoon, similar to that found in Hydrobiosidae.

The family, previously regarded as a subfamily of Rhyacophilidae, occurs in all faunal regions and there are about 20 genera with 400 species. Glossosomatids are well represented in eastern Australia and New Guinea, and present on some other south-western Pacific islands, but do not occur in W.A. or New Zealand (Neboiss 1986a). All south-western Pacific-Australian region species are referred to *Agapetus*.

**3. Hydroptilidae.** This is a large family, commonly known as the micro-caddises; they are the smallest of all

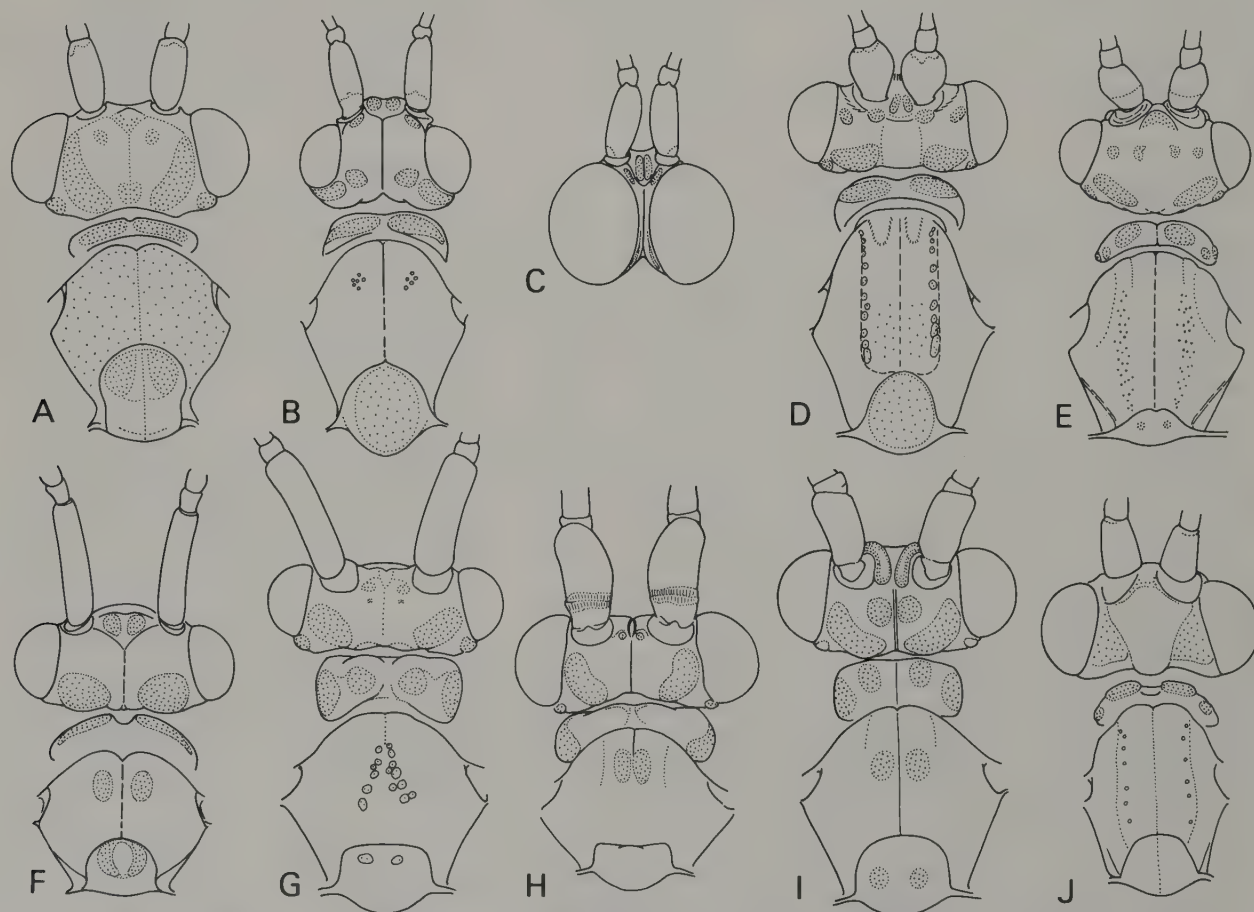


Fig. 40.6 Dorsal view of adult head, pro- and mesonota: A, *Helicophya delamarei*, Helicophidae; B, *Marilia* sp., Odontoceridae, ♀; C, *Marilia* sp., Odontoceridae, ♂ head; D, *Atriplectides dubius*, Atriplectididae; E, *Anisocentropus bicoloratus*, Calamoceratidae; F, *Helicopsyche* sp., Helicopsychidae; G, *Tasmanthrus angustipennis*, Philorheithridae; H, *Austrheithrus* sp., Philorheithridae; I, *Aphilorheithrus stepheni*, Philorheithridae; J, *Triplectides australis*, Leptoceridae.

[R. Plant]



Trichoptera with wing span 4–12 mm. Ocelli either present or absent according to genus. Maxillary palps 5-segmented in both sexes, first 2 segments very short, and apical segment simple. Antennae shorter than fore wing; shorter in females than in males; basal segment shorter than head. Mesoscutum without setal warts, scutellum flat, triangular, pointed posteriorly, margins vertical (Fig. 40.5C). Wings elongate, slender, usually acute apically (Fig. 40.7D), densely covered with fine pubescence, hind wing fringe with very long hairs, longer than width of wing; wing venation reduced, interpretation of veins often very difficult. Tibial spurs variable: 0–1:2–3:3–4.

Larvae during the first 4 instars are small, slender and free living. In the 5th instar a purse-shaped case is constructed and the abdomen becomes enlarged (Figs 40.11L, M). Heavily sclerotised plates present on all 3 thoracic nota; mid and hind legs often longer than fore legs; anal claws small. Larval case usually laterally, but sometimes dorsoventrally, flattened; constructed either of small sand grains, algae, other plant material or entirely of silk. Before pupation the larva attaches the case to the substrate.

The family is known from all faunal regions and there are about 80 genera with 650 species. Known throughout Australia and represented by 12 genera with 101 species (Wells 1983, 1985).

### Superfamily HYDROPSYCHOIDEA

Adults with 5-segmented maxillary palps in both sexes, terminal segment annulate and flexible, usually at least twice as long as preceding segment. Antennae with basal segment stout, shorter than head, flagellum slender, often slightly to considerably longer than fore wing. Females with single anal-vaginal opening, abdominal segment 10 with pair of cerci.

Larvae are mostly stationary, construct fixed shelters, retreats or filter nets (Cartwright and Dean 1982); antennae very small; thorax with sclerotised nota on all segments or on prothorax only; legs generally of equal length; abdomen lacking dorsal and lateral spacing humps on segment 1, lateral fringe may be present, without dorsal sclerite on segment 9, anal prolegs free, well developed, anal claw large.

Lepneva's (1956) subdivision of the former Psychomyiidae into three families (Psychomyiidae *s.str.*, Ecnomidae and Polycentropodidae) has been followed by most authors and is adopted below.

**4. Philopotamidae.** Adults small to medium sized with wing span 12–20 mm; often dark, blackish or mottled greyish brown. Ocelli present. Maxillary palps 5-segmented in both sexes, segment 2 with mesodistal brush of setae; segment 5 long, flexible. Mesoscutum without setal warts, although sometimes with small groups of setae; scutellum usually with pair of warts (Fig. 40.5D), these sometimes fused medially forming single setal wart. Wings elongate, ovate, venation complete (Fig. 40.7H), discoidal cell closed in both wings, median cell closed only in fore wing; small hyaline areas at cross-veins and at arculus in fore wing.

Larvae slender (Figs 40.11N–T), pale yellowish with

sclerotised parts of the head and pronotum orange, posterior margin thickened, black; labrum membranous, T-shaped (Fig. 40.11P), anterolateral margins angular; meso- and metanota membranous. Abdominal gills and lateral fringe absent, anal papillae present (Fig. 40.11O); anal claws simple, without accessory hooks (Fig. 40.11T). Larvae live in soft, silken tubes or sack-like nets on underside of rocks in running waters. They feed on algae and fine organic particles which are swept by water currents into the larval nets and there picked up by the larva with its specialised labrum.

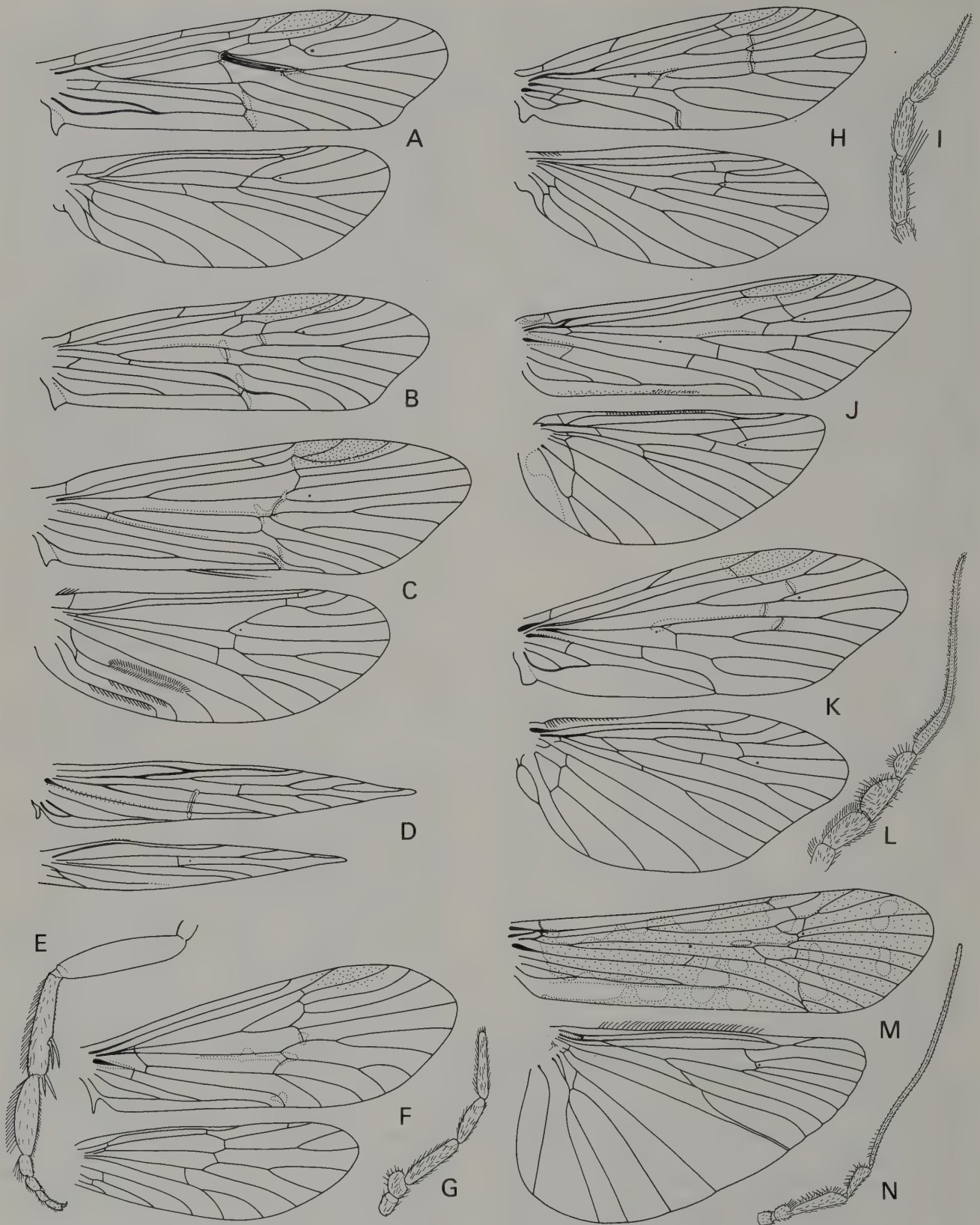
The family occurs in all faunal regions. Approximately 12 genera with 400 species are known, and of those 5 genera with 19 species have been recorded from Australia.

**5. Stenopsychidae.** Adults medium to moderately large with wing span 18–35 mm, often with colourful black and golden wing pattern (Fig. 40.1B). The Australian species are all assigned to the endemic *Stenopsychodes* which differs from the other genera by the absence of ocelli. Maxillary palps 5-segmented in both sexes, segment 2 with apical brush of bristles, and segment 5 longer than all other segments combined. Antennae rather robust, about as long or slightly longer than fore wing, basal segment short. Mesoscutum with pair of rounded setal warts, separated by anteriorly produced mesal section of scutellum (Fig. 40.5E); scutellum with single mesal wart. Wing venation complete, regular and similar in both sexes; discoidal and median cells closed in both wings (Fig. 40.8A). Tibial spurs 3:4:4.

Larvae of the Australian species are unknown but specimens believed to belong here resemble Polycentropodidae. Three genera with about 70 species are known from Ethiopian, Asian Palaearctic, Oriental and Australasian regions. *Stenopsychodes* is well represented on Cape York Peninsula but is not known from New Guinea.

The genus *Stenopsychodes* was described in the family Polycentropodidae by Ulmer (1916), retained there by Mosely and Kimmins (1953), placed in the family Psychomyiidae by Riek (1970) but transferred to the family Stenopsychidae by Schmid (1969).

**6. Hydropsychidae.** A large family, found throughout the world in a great variety of habitats; some species small, but the majority medium to rather large with wing span 8–40 mm (Fig. 40.1C). Ocelli absent. Maxillary palps (Figs 40.7L, N) 5-segmented in both sexes, but reduced or absent in certain genera of Macronematinae; segment 5 usually as long as, or even longer than, the other 4 segments together (Fig. 40.7N), in a few genera about the same length as segment 4. Antennae slender, filiform, about as long as fore wing, except in Macronematinae, where they are much longer. Mesoscutum without setal warts; scutellum with one median setal wart (Figs 40.5F, G). Wing venation complete; discoidal and median cells closed in fore wing; hind wing from slightly to much wider than the fore wing (Figs 40.7J, K, M). S5 in both sexes of many taxa with slender lateral filament, lobe or obtuse projection, with aperture of internal gland apically. Males of some genera with pair of large, reticulated, membranous, internal sacs in abdominal segments 6





and 7; their functions are not known. Tibial spurs variable 0-2:2-4:2-4.

Larvae (Figs 40.12A-I) construct fixed retreats of plant and rock fragments; a capture net is constructed in front to strain food particles from flowing water, therefore almost all species are confined to a variety of lotic water habitats. Thoracic segments covered with sclerites; abdominal segments with lateral and ventral abdominal gills, branched from a single basal stalk. Abdominal segments covered with fine setae; anal prolegs project freely from abdomen, claws with brush of long setae (Fig. 40.12B). Two groups of fine transverse ridges (Fig. 40.12E) present on the ventral surface of the head in most species; ridges produce sound when rubbed by the raised edge of the fore femur. Larvae feed on algae, organic particles and small invertebrates captured in the nets. The pupal chamber is constructed from small stones and sand grains, sometimes incorporating plant debris; the inner lining is spun into a soft silken cocoon.

The family is known from all faunal regions; it is subdivided into 3 subfamilies—HYDROPSYCHINAE, DIPLECTRONINAE and MACRONEMATINAE—and contains more than 900 species in 50 genera, of which 27 species in 10 genera, representing all three subfamilies, occur in Australia.

**7. Polycentropodidae.** Adults small to medium sized, rather stockily built; wing span 8–25 mm; usually dark brown, mottled with whitish to cream or golden spots. Ocelli absent. Maxillary palps 5-segmented in both sexes, 1st and 2nd segments short, each shorter than 3rd; 3rd arises before apex of 2nd, apical segment long, annulated, flexible (Fig. 40.8c). Antennae stout, about as long or slightly shorter than fore wing, individual segments short. Mesoscutum with pair of rounded setal warts, and sometimes setiferous punctures; scutellum with single rounded mesal wart (Fig. 40.5H). Fore wings moderately broad, densely pubescent, discoidal and median cells closed;  $R_1$  not forked apically (Figs 40.8B, D). S5 with lateral filaments. Tibial spurs 3:4:4; in females mid tibia usually flattened.

Of several subfamilies recognised by some authors (Malicky 1973; Wiggins 1977) only POLYCENTROPODINAE and HYALOPSYCHINAE are known from Australia. Adult Hyalopsychinae (Schmid 1980 considers it a family) are characterised by large eyes (Fig. 40.5i), particularly in males, smaller in females; maxillary palps reduced, apical segment short, not annulate; labial palps absent. Larvae of Hyalopsychinae are unknown. In Australia only one species is recorded, from North Qld (Neboiss 1980).

Larvae (Figs 40.12J–N) with only pronotum sclerotised; meso- and metanota membranous or at most each with partially sclerotised plate, fore trochantin acute; abdominal segments without gills, but anal papillae present in some groups; lateral fringe present; anal prolegs very

long, diverging, claws often with slender accessory hooks and acute tooth-like points on their concave edge. Larvae occur in diverse lotic and lentic habitats and construct a variety of silken capture nets or tubular retreats with flared opening. Feeding habits variable: even within one genus there may be filter feeders, shredders or predators.

The family is known from all faunal regions, with 25 genera and approximately 300 species; in Australia 6 genera with 12 species are recorded.

**8. Ecnomidae.** Adults mostly small to medium sized; wing span 6–18 mm; usually dull greyish brown, mottled. Ocelli absent. Maxillary palps 5-segmented in both sexes; segment 2 longer than segment 1 and about as long as 3, apical segment flexible. Antennae at most as long as fore wing. Mesoscutum and scutellum each with pair of rounded setal warts (Fig. 40.5j). Wings narrow, rounded apically; fore wing  $R_1$  usually forked at apex (Fig. 40.8F); discoidal and median cells closed. S5 without lateral filaments; female abdomen terminates bluntly or with elongate ovipositor (*Ecnomina*). Tibial spurs 2:4:4 or 3:4:4.

Larvae (Figs 40.12O–R) with all thoracic nota sclerotised; pronotal sclerite extended posteroventrally; fore trochantin elongate, acute apically; abdomen without gills; lateral setal fringe present; anal legs long, claws curved, narrow, with ventral comb of minute spinules along concave margin. Larvae construct fixed tubes of silk, incorporating particles of plant and mineral origin; they feed upon organic particles. Habitat in lentic and lotic waters.

The family occurs in all faunal regions. Seven genera with more than 100 species are known, of which 2 genera with 56 named species are recorded from Australia.

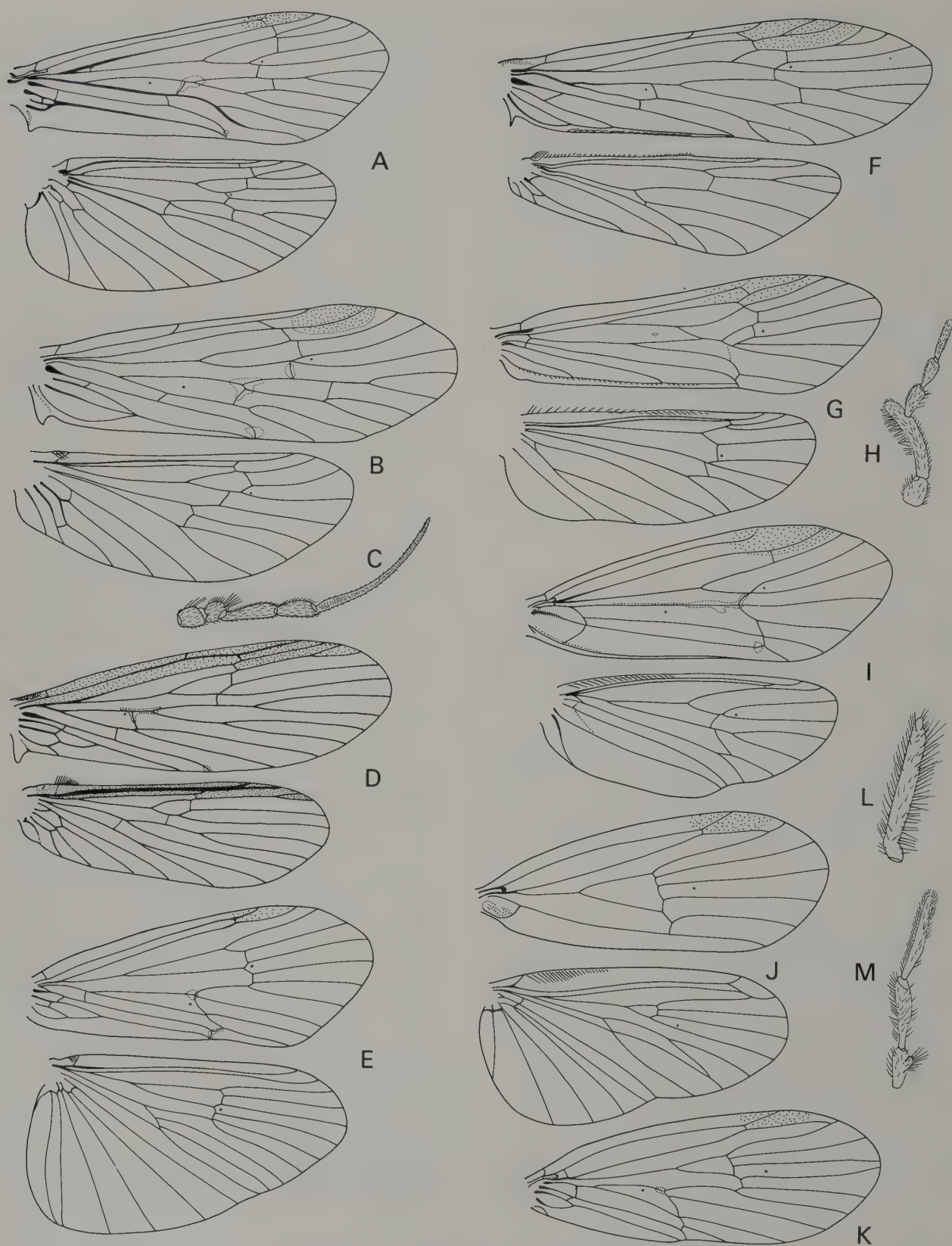
**9. Psychomyiidae.** Adults small to moderately small; wing span 5–9 mm; usually dull, dark grey. Ocelli absent. Maxillary palps 5-segmented in both sexes; segment 3 never inserted before the apex of segment 2; segment 5 as long as segments 3 and 4 together, annulate, flexible. Antennae moderately robust, not exceeding length of fore wing. Mesoscutum with pair of ovoid setal warts. Wings slender, rounded or tapered apically; fore wing  $R_1$  not forked apically, fork 1 absent, discoidal cell short, median cell closed or open, thyridial cell very small, close to wing base and usually distinctly separated from base of median cell. Hind wing narrow, lanceolate, costal margin more or less produced anteriorly at middle, venation reduced. S5 without lateral filament; female abdomen usually terminates with elongate ovipositor. Tibial spurs 2:4:4.

Larvae of Australian species are not known.

The family occurs in all faunal regions except Neotropical. Approximately 15 genera with about 150 species are known; 2 genera with one species each are now recorded from Australia. [Neboiss 1990]

Fig. 40.7 Wings (A, C, D, F, H, J, K, M), fore wing (B), mid leg (E) and maxillary palps (G, I, L, N) of adults: A, *Apsilochorema gisbum*, Hydrobiosidae-Apsilochoreminae, ♂; B, *A. gisbum*, ♀; C, *Taschorema asmanum*, Hydrobiosidae-Hydrobiosinae, ♂; D, *Hydroptila scamandra*, Hydroptilidae; E, *Agapetus* sp., Glossosomatidae, ♀; F, *Agapetus tasmanicus*, Glossosomatidae; G, *Agapetus* sp., Glossosomatidae; H, *Hydrobiosella waddama*, Philopotamidae; I, *Chimarra* sp., Philopotamidae, ♂; J, *Cheumatopsyche modica*, Hydropsychidae-Hydropsychinae; K, *Austropsyche victoriana*, Hydropsychidae-Diplectroninae; L, *A. victoriana*, ♂; M, *Baliomorpha pulchripenne*, Hydropsychidae-Macronematinae; N, *Baliomorpha banksi*, Hydropsychidae-Macronematinae, ♂.

[R. Plant]





### Superfamily LIMNEPHILOIDEA

Adults with maxillary palps 5-segmented in females, but number of segments frequently lower in males; terminal segment similar in structure to preceding segments, not annulate, except some Leptoceridae with last one or 2 segments incompletely sclerotised and granular in appearance. Antennae with basal segment often enlarged, longer than head or modified in shape, provided with sensory hairs; flagellum from about length of fore wing to much longer. Females with separate anal and vaginal openings; without cerci on segment 10.

Larvae mobile, construct portable tubular cases from plant or mineral materials; head with peg-like antennae situated between eye and anterior margin of head; thorax with pronotum sclerotised, mesonotum either sclerotised or with several paired sclerotised plates; fore legs short, mid and hind legs longest; abdominal segment 1 usually with dorsal and lateral spacing humps; segment 9 usually with dorsal sclerite, anal prolegs short, bases fused with abdomen, anal claw usually with small dorsal accessory hook or hooks.

**10. Limnephilidae.** To this family belong some of the largest Australian species (Fig. 40.1D) with wing span 25–40 mm; wings broad, yellowish brown, without distinct pattern. Ocelli present. Maxillary palps 3-segmented in male, 5-segmented in female, slightly pubescent; labial palps small. Antennae as long as, or slightly shorter than fore wing, basal segment enlarged. Mesoscutum with pair of small setal warts (Australian species); scutellum with either pair of separate or one continuous mesal wart (Fig. 40.5L). Fore wing with discoidal cell closed; median cell absent; anal veins fused; hind wing usually broader than fore wing (Fig. 40.8E). Tibial spurs 1:2:2 (Australian species); tibiae and tarsi usually armed with several rows of strong dark spines.

Larval head (Figs 40.13C, D) with antennae midway between eye and anterolateral margin of head capsule. Prosternal horn present; mesonotal sclerites usually not subdivided; metanotum with 2 or 3 pairs of small sclerites (Fig. 40.13E). Abdominal gills branched; lateral fringe present; row of bifid spicules above lateral fringe on most abdominal segments but absent from segment 8. Larval case tubular, constructed of combinations of plant and mineral materials. All Australian species are found in small to medium-sized, fast-flowing, montane streams; larvae feed on detritus and fine organic particles.

Large family, widely distributed in the cooler regions of Palaearctic and Nearctic from which about 130 genera with more than 1000 species are recorded. In Australia, only one genus with 3 species is known, restricted to the south-east, including Tas.

**11. Plectrotarsidae.** Adults (Fig. 30.1E) small to medium sized; wing span 10–22 mm. Ocelli present. Maxillary palps 3-segmented in male, 5-segmented in female. Antennae stout, about as long as fore wing. Mouth-parts either normal or forming an elongate proboscis. Meso-

scutum with 2 parallel bands of setiferous punctures mesally and 2 small groups posteriorly on either side of scutellum; setal warts on scutellum connected mesally, elongate or rounded (Fig. 40.5N). Wings broad, rounded apically and densely pubescent; discoidal cell closed, small; hind wing with several strong frenular bristles at base, vein  $R_1$  joins  $R_2$  near wing margin (Fig. 40.9B). Tibial spurs 1–2:2–4:4.

Larval head (Figs 40.13N, O) only slightly longer than wide, antenna about midway between eye and anterolateral margin of head capsule; ventral apotome broadly triangular, lateral margins distinctly convex, entirely separating genae. Pronotum (Fig. 40.13P) short with transverse elliptical bulge; prosternal horn rather small, pale and membranous; meso- and metanota each with 3 pairs of sclerites, those on metanotum rather indistinct; legs stout. Abdominal gills single or branched; lateral fringe present; segment 8 without lateral row of bifid spicules, segment 9 with dorsal sclerite; anal claws with 2 accessory hooks. Larvae construct rather untidy tubular cases from irregularly criss-crossed, short pieces of cut vegetation (Fig. 40.15D) and inhabit shallow, vegetation-rich lakes and swamps (Neboiss 1987b). Adults fly during daytime in bright sunshine in a moth-like manner around flowering shrubs (*Leptospermum*, *Melaleuca* and others).

This endemic Australian family contains 3 genera with 5 species and is restricted to south-eastern and south-western mainland Australia and Tas.

**12. Oeconesidae.** Adults moderately large to large with brown mottled wings (Fig. 40.1F) of 30–40 mm span; wings at rest folded flat over body. Ocelli absent. Maxillary palps 1- or 2-segmented in males (Australian genus 1-segmented) (Fig. 40.8L), 5-segmented in females. In Australian genus segment 1 of labial palp with short, rounded, apicomeresal projection (Fig. 40.8M). Antennae about as long as or slightly longer than fore wing, basal segment shorter than head. Mesoscutum with pair of elongate setal warts, scutellum with median wart (Fig. 40.5M). Wings broad, rounded apically, venation sexually dimorphic, often reduced or modified in males; vein  $R_1$  joins  $R_2$  close to wing margin; discoidal cell closed (Figs 40.8J, K). Tibial spurs 2:4:4.

Larval head (Figs 40.13K, L) in frontal view almost circular, entirely surrounded by well developed carina; antennae close to eyes; ventral apotome broadly triangular, entirely separating the genae. Pronotum strongly sclerotised, short, with transverse elliptical bulge on each side; prosternal horn absent in Australian species, present in some New Zealand species; meso- and metanota each with 3 pairs of sclerites (Fig. 40.13M). Abdominal gills single or branched; lateral fringe present; segment 8 without lateral row of bifid spicules, anal claw with 2 or 3 accessory hooks. Larvae are detritivores and inhabit small, fast-flowing streams in forested areas; their cases (Fig. 40.15B) are constructed of irregular pieces of plant material.

Fig. 40.8 Wings (A, B, D, E, F, G, I, J), fore wing (K), maxillary palps (C, H, L) and labial palps (M) of adults: A, *Stenopsychodes mjobergi*, Stenopsychidae; B, *Nyctiophylax repandus*, Polycentropodidae-Polycentropodinae; C, *Plectrocnemia australica*, Polycentropodidae-Polycentropodinae, ♂; D, *Hyalopsyche disjuncta*, Polycentropodidae-Hyalopsychinae; E, *Archaeophylax ochreus*, Limnephilidae; F, *Ecnomus tillyardi*, Ecnomidae; G, H, *Philanisus plebeius*, Chathamidae, ♂; I, *Tasimia palpata*, Tasimiidae; J, *Tascuna ignota*, Oeconesidae, ♂; K, *T. ignota*, ♀; L, *T. ignota*, ♂; M, *T. ignota*, ♂. [R. Plant]





The family is restricted to Australia and New Zealand with a total of 6 genera and 16 species; the only Australian species is endemic to Tas.

**13. Tasimiidae.** Moderately small to medium sized, dark, inconspicuous adults with wing span 12–18 mm. Ocelli absent. Maxillary palps 4-segmented in males (Australian species), 5-segmented in females. Antennae slightly longer than fore wing, basal segment longer than head. Eyes covered with short setae. Mesoscutum with pair of rounded setal warts (Fig. 40.5s), separated from the median line; scutellum with pair of elongate warts, sometimes fused. Wings rather broad, rounded apically, fore wing with discoidal cell open, anal veins and jugal lobe reduced (Fig. 40.8t). Tibial spurs 2:4:4. Adults resemble Conoesucidae in general appearance.

Larval head (Fig. 40.13A) with antennae midway between eye and anterolateral margin of head capsule; eyes bulging; ventral apotome triangular, only partially separating the genae. Anterolateral angles of pronotal sclerite extended, acute (Fig. 40.13b); mesonotal sclerites not subdivided; metanotum with pair of small sclerites only. S1 with median pair of bristles, abdominal gills as single filaments; lateral fringe well developed. Dorsal sclerite present on segment 9. Larval case tubular, constructed of small stones with larger pieces along sides (Fig. 40.15A). Larvae inhabit clear, fast-flowing streams.

The family is known from Australasian and Neotropical regions with 2 genera in each and a total of 8 species, of which 6 are in Australia. The Australian species are restricted to the eastern part of the mainland and Tas.

**14. Chathamidae.** Adults are rather slender, medium sized with pale yellowish grey mottled wings, wing span 15–22 mm. Ocelli absent. Maxillary palps 5-segmented in both sexes, in males segment 2 is long, segment 3 arises before apex of 2 (Fig. 40.8h). Antennae stout, basal segment shorter than head. Mesoscutum mostly with fine setiferous punctures, arranged in 2 irregular bands (Fig. 40.5k); scutellum rounded anteriorly, with pair of indistinctly fused setal warts. Wing coupling by enlarged, curved macrotrichia on fore margin of hind wing; fore wing with reduced jugal lobe (Fig. 40.8g). Mid tibia distinctly longer than femur. Female abdomen terminates in long ovipositor. Tibial spurs 2:2:4.

Larva (Figs 40.12s–v) a portable tube-case maker; head broadly ovoid, labrum with numerous secondary setae; mesonotum with pair of weakly sclerotised plates; metanotum with 3 pairs of weak sclerites, covered with numerous setae; distinct patch of setae present on metasternum and also on S1. Abdomen with branched gills, without lateral fringe, segment 8 with lateral row or irregular band of fine spicules. The larvae inhabit intertidal rock pools, feeding mainly on coralline marine algae. The adults fly at dusk along open ocean shores low to the ground between waterline and shore vegetation; they shelter behind rocks.

The family is restricted to the Australian and New Zealand areas with a total of 4 species in 2 genera. *Philanisus plebeius*, the only Australian species, also occurs in New Zealand (Riek 1977a).

**15. Conoesucidae.** Adults small to medium sized with wing span 10–25 mm, blackish brown to black, usually found amongst vegetation on the banks of fast-flowing, small to medium-sized streams. Ocelli absent. Maxillary palps of males 1–3-segmented, often partly or entirely membranous, held upright in front of face; in females maxillary palps 5-segmented. Antennae stout, about as long as, or slightly shorter than fore wing, basal segment long. Pronotum with pair of transverse, elongate setal warts; mesoscutum without setal warts, but with deep anteromesal fissure; scutellum with pair of setal warts (Fig. 40.5t). Both wings about equal in width, elongate ovate; jugal lobe well developed; discoidal cell present, venation sexually dimorphic (Figs 40.9e, f). Tibial spurs 2:2:2–4.

Larval head (Figs 40.13Q, R) with antennae usually situated close to anterior margin of head, not further back than midway between eye and anterior margin; ventral apotome quadrate, posterolateral margins indistinct. Mesonotum almost entirely covered with sclerites; metanotum with one or 2 pairs of small sclerites, anteromesal setal area with no more than 2 setae (Fig. 40.13s). Abdominal segment 1 with dorsal hump reduced; gills present or absent; lateral fringe absent; segment 8 with lateral row of bifid spicules; segment 9 with dorsal sclerite; anal claw with small, accessory hook. Larvae construct cylindrical, only slightly curved, tube-cases of small stones, sand grains and plant material or silk (Fig. 40.15e). Larvae live in fast-flowing, clear streams, and feed on algae, moss and other plants or plant detritus.

The family is restricted to the south-western Pacific-Australian region, where it is widespread in New Zealand, eastern mainland Australia and Tas. There are 13 genera with more than 30 species of which 6 genera with 21 species are recorded from Australia.

**16. Antipodoeciidae.** A family known from one small, dark species with wing span 8–10 mm. Ocelli absent. Maxillary palps 3-segmented in male, curved and held upright in front of face, apical segment short; in female maxillary palps 5-segmented. Antennae about as long as fore wing, basal segment short, about half as long as head, posterior setal warts large, rounded. Mesoscutal setal warts small, oval, often indistinct; scutellum with median, dome-shaped wart (Fig. 40.5r). Wings slender, pointed apically; discoidal and median cells absent; large hyaline area in centre of wing at anastomosis; anterior margin of hind wing with sparse long bristles on basal half (Fig. 40.9c). Tibial spurs 2:2:4; mid leg with a row of short, dark spines on femur, tibia and tarsus.

Larval head (Figs 40.13t, u) almost circular in frontal view, frontoclypeal apotome broad, antennae about midway between eyes and anterior margin of head capsule; labrum prominent; ventral apotome indistinct, triangular, genae almost abutting at occipital foramen. Pronotal sclerite with anterolateral angles distinctly extended, acute (Fig. 40.13v); meso- and metanotal sclerites indistinct, legs stout. Abdominal gills and lateral fringe absent; anal prolegs usually with one accessory hook. Larval case tubular, slightly curved, constructed of small sand grains (Fig. 40.15f).

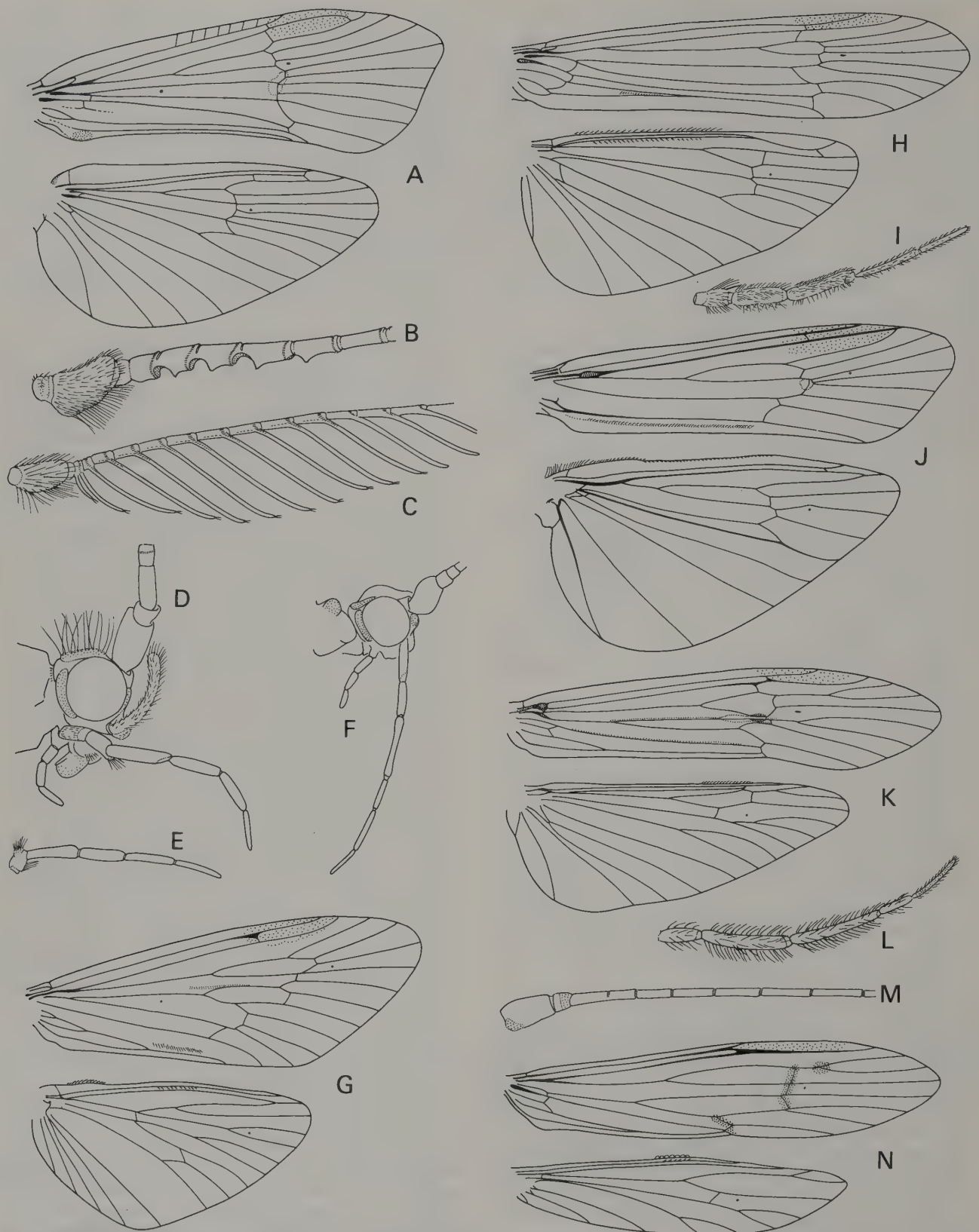


Fig. 40.10 Wings and other structures of adults: A, *Aphilorheithrus stepheni*, Philorheithridae, wings, ♂; B, *Austrheithrus glymma*, Philorheithridae, basal section of antenna, ♂; C, *Ramiheithrus virgatus*, Philorheithridae, basal section of antenna, ♂; D, *Aphilorheithrus stepheni*, Philorheithridae, head, lateral, ♂; E, same, maxillary palp; F, *Anisocentropus bicoloratus*, Calamoceratidae, head, lateral, ♂; G, *A. bicoloratus*, Calamoceratidae, wings; H, *Atriplectides dubius*, Atriplectididae, wings; I, *A. dubius*, maxillary palp, ♀; J, *Marilia* sp., Odontoceridae, wings; K, *Triplectides truncatus*, Leptoceridae, wings, ♂; L, *Triplectides australis*, Leptoceridae, maxillary palp, ♂; M, *T. australis*, antenna, ♂; N, *Oecetis minasata*, Leptoceridae, wings, ♂.

[R. Plant]



The only known species is restricted to eastern Australia; it is not known from Tas.

**17. Helicopsychidae.** Adults mostly small, greyish brown to black with rather slender wings; wing span 10–16 mm. The integument of at least the first few abdominal sterna has a reticulate pattern. Ocelli absent. Maxillary palps 2- or 3-segmented in males, 5-segmented in females. Head with large, ovoid, posterior setal warts. Mesoscutum with pair of small, rounded setal warts (Fig. 40.6F); scutellar warts often merge mesally into one. Wings narrow, coupled by row of hamuli; discoidal cell closed in fore wing, open in hind wing (Fig. 40.9I). Tibial spurs 2:2:4 (Australian species).

Larval head with labrum prominent (Figs 40.14N, O), pro- and mesonotal sclerites well developed, metanotal sclerites small. Abdominal gills short and few in number; anal claw with comb-like row of teeth (Fig. 40.14M). Larvae construct helical, snail-shell-like cases of sand grains (Fig. 40.14L) and live in lotic and lentic waters from cool, fast-flowing streams to warm, littoral zones of lakes. The larvae feed mainly on algae and fine organic material.

The family is known from all faunal regions with 6 genera and approximately 100 species, of which one genus with 6 species is known from Australia.

**18. Calocidae.** Most of the adults in this family are medium sized with wing span 12–25 mm; a few are moderately large, reaching 30 mm; fore wings blackish, usually mottled with whitish or yellowish irregular spots. Ocelli absent. Maxillary palps 3–5-segmented in males, frequently modified; 5-segmented in females. Antennae stout, about as long or slightly shorter than fore wing; basal segment long, in males often with expanded lobes or other modifications (Figs 40.9G, H). Dorsum of head, mesally in some genera with eversible membranous filaments and long posterior setal warts (Fig. 40.5P); in females posterior setal warts shorter. Pronotum usually with 2 pairs of setal warts, mesal pair small, rounded, lateral ones elongate (except in males of *Caenota*, which have only one pair of elongate warts, similar to those in *Conoesucidae*). Mesoscutum without setal warts; scutellum with pair of elongate warts (Fig. 40.5Q). Fore wings elongate, ovate, discoidal cell closed, venation usually differing in sexes (Fig. 40.9I). Tibial spurs 2:2:4.

Larval head with antennae close to anterior margin of eye; mesonotal sclerites reduced posteriorly; metanotum with 4 or more setae in each anteromesal setal area (Figs 40.13W–Y). Abdominal segment 1 with dorsal and lateral spacing humps reduced; gills and lateral fringe absent; segment 8 with lateral row of bifid spicules; segment 9 without dorsal sclerite. Larvae construct slightly curved tube-cases from sand grains or pieces of plant debris (Figs 40.15G, H); they inhabit small, cool streams in forested areas. One Tas. species has terrestrial larvae.

Until recently the family was part of the Sericostomatidae. It contains 7 genera with 20 species and is restricted to Australia and New Zealand. Five genera with 18 species are known from Australia.

**19. Helicophidae.** Adults of this family are small to medium sized, inconspicuous, dark greyish with wing

span 8–15 mm. Ocelli absent. Maxillary palps 5-segmented in both sexes. Antennae not exceeding length of fore wing, basal segment about as long as head. Large, linear, posterolateral setal warts on head. Pronotum with pair of transversely elongate warts; mesoscutum without setal warts; scutellum with one or a pair of small setal warts (Fig. 40.6A). Fore wing elongate oval, with or without discoidal cell, jugal lobe reduced, venation often differing in sexes; hind wing with row of hamuli along basal half of anterior margin, large vein-free area discally (at centre of wing) (Fig. 40.9D). Tibial spurs 2:2:4.

Larvae with more or less developed anterolateral carina on dorsum of head; antennae about midway between eye and anterior margin of head capsule (Fig. 40.14D). Mesonotum with reduced sclerites; metanotal sclerites small (Fig. 40.14E); abdominal segment 1 with dorsal and lateral spacing humps; gills, lateral setal fringe and sclerite on segment 9 all absent; lateral band of bifid spicules on segment 8; claw of anal proleg with single accessory hook. Larvae construct slightly curved, cylindrical tube-cases of sand grains (Fig. 40.15I) or plant fragments, and are known from clear, swift-flowing streams in forested areas.

The family is restricted to Australia and New Zealand, where a total of 3 genera and 8 species are known, of which 2 genera and 6 species are recorded from Australia.

**20. Kokiriidae.** Adults (Fig. 40.1G) are stockily built, medium-sized, with wing span 14–24 mm, dark brown or blackish. Ocelli absent. Maxillary palps 3-segmented in male, 5-segmented in female. Antennae stout, about as long as fore wing. Mouth-parts more or less elongate, sometimes forming a proboscis. Mesoscutum and scutellum each with pair of setal warts (Fig. 40.5O). Fore wing vein  $R_1$  joined to Sc basad of pterostigma by short cross-vein or sharp bend;  $R_2$  and  $R_3$  frequently fused; discoidal cell closed; in hind wing  $R_1$  incomplete, terminating before reaching wing margin; discoidal cell open (Fig. 40.9A). Tibial spurs 1:4:4 or 2:4:4.

Larval head strongly dome-shaped; antennae rather long, close to anterior margin of head capsule; eyes large, elongate (Fig. 40.13I); ventral apotome somewhat triangular, entirely separating genae. Fore and mid legs similar in form with tibia and tarsus fused into single segment, hind legs long (Figs 40.13F–H). Thoracic sclerotisations weak (Fig. 40.13J). Abdominal segment 1 without dorsal spacing hump but lateral humps prominent; abdominal gills branched; lateral fringe present; segment 8 without lateral row of bifid spicules; anal claws with several accessory hooks. Larvae construct tubular, sand grain cases, somewhat depressed dorsoventrally, with lateral flanges (Fig. 40.15C). Their habitat is sandy substrates in streams and lakes.

The family is restricted to Australasian and Neotropical regions with 6 genera and 8 species, of which 3 genera with 5 species are known from Australia.

**21. Philorheithridae.** Adults moderately large, wing span 16–35 mm. Wings irregularly speckled. Ocelli absent. Maxillary palps 3–5-segmented in males, 5-segmented in females; basal segment short with apicomeral expansion bearing tuft of setae. In most genera males

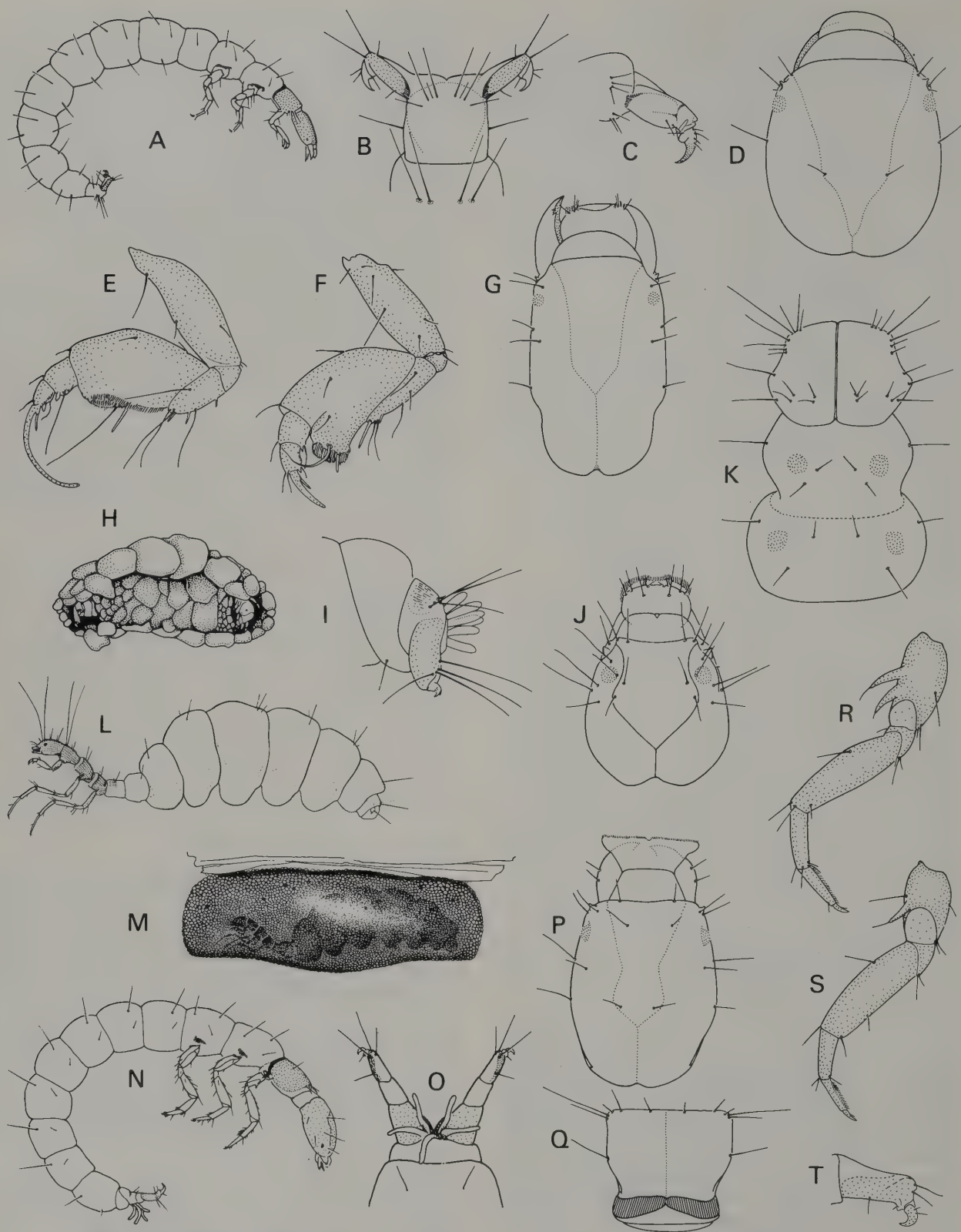


Fig. 40.11 Larvae: A, Hydrobiosidae, lateral; B, same, apical abdominal segments, dorsal; C, same, anal proleg, lateral; D, *Apsilochorema* sp., Hydrobiosidae-Apsilochoreminae, head, dorsal; E, same, fore leg; F, *Ulmerochorema* sp., Hydrobiosidae-Hydrobiosinae, fore leg; G, *Taschorema* sp., head, dorsal; H, *Agapetus* sp., Glossosomatidae, case with larva; I, same, apical abdominal segments, lateral, showing abdominal proleg and anal papillae; J, same, head dorsal; K, same, thoracic segments dorsal; L, *Hellyethira* sp., Hydroptilidae, lateral; M, same, larval case; N, Philopotamidae, lateral; O, same, apical abdominal segments, dorsal; P, same, head, dorsal; Q, same, pronotum, dorsal; R, *Hydrobiosella* sp., Philopotamidae, fore leg; S, *Chimarra* sp., Philopotamidae, fore leg; T, same, anal proleg, lateral.

[R. Plant, A. Neboiss]



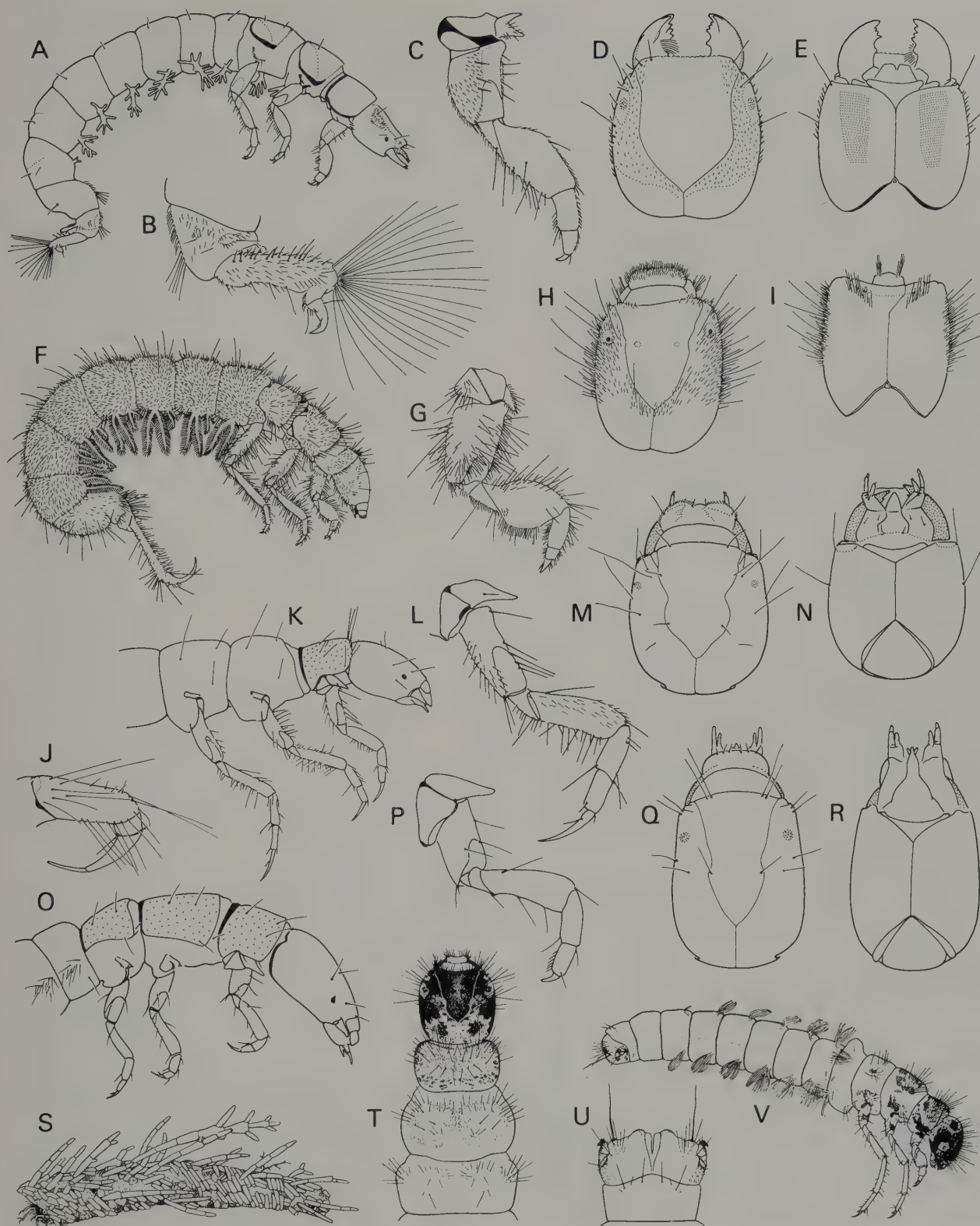
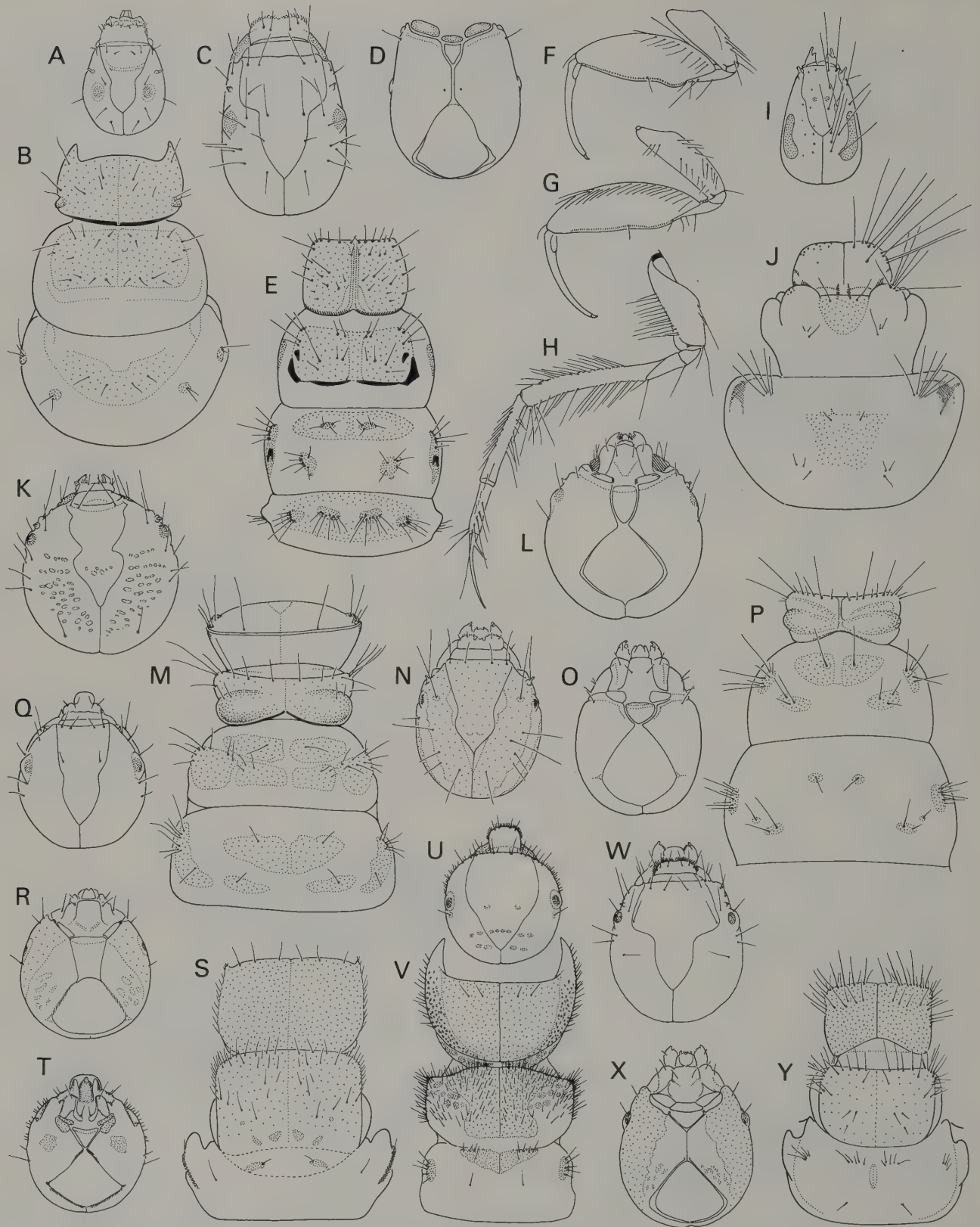


Fig. 40.12 Larvae: A, *Cheumatopsyche* sp., Hydropsychidae-Hydropsychinae, lateral; B, same, anal proleg; C, same, fore leg, trochantin forked; D, same, head, dorsal; E, same, head, ventral, showing stridulatory ridges; F, *Baliomorpha pulchripenne*, Hydropsychidae-Macronematinae, lateral; G, same, fore leg, trochantin simple; H, same, head, dorsal; I, same, head, ventral, incomplete ecdysial line on one side; J, *Plectrocnemia* sp., Polycentropodidae, anal proleg; K, same, head and thoracic segments, lateral; L, same, fore leg and trochantin; M, same, head, dorsal; N, same, head, ventral; O, *Ecnomus* sp., Ecnomidae, head and thoracic segments, lateral; P, same, fore leg and trochantin; Q, same, head, dorsal; R, same, head, ventral; S, *Philanisus plebeius*, Chathamidae, larval case; T, same, head and thoracic segments, dorsal; U, same, apical abdominal segments, dorsal; V, same, lateral.

[A–R by R. Plant, S–V by M. Quick]





with pair of pilifers arising above base of maxillary palps and held upright in front of face (Fig. 40.10D). Antennae stout, about as long as fore wing; 10–15 basal segments often excavated laterally, bearing setae or pectinate (Figs 40.10B, C). Mesonotum usually with setal warts, if warts absent, then one or several setiferous punctures present in their place; scutellum usually with pair of rounded setal warts (Figs 40.6G–I). Wings elongate (Fig. 40.10A), in some species truncate apically; discoidal cells closed in both wings; in fore wing  $R_1$  joins  $R_2$  near apical margin; in resting position wings folded longitudinally. Tibial spurs 2:4:4.

Larval head (Figs 40.14F, G) with antennae close to anterior margin; ventral apotome triangular, not separating genae. Pro- and mesonota fully sclerotised, prosternum with sclerite; metanotum with 2 or 3 pairs of sclerites (Fig. 40.14H). Fore and mid legs subequal, semi-raptorial; mid leg with tibia and tarsus fused; hind legs long, normal (Fig. 40.14I). Abdominal segment 1 with dorsal and lateral spacing humps; gills branched; lateral fringe present; segment 8 with row of bifid spicules, dorsal sclerite present on segment 9; anal claw with single accessory hook. Larvae are predatory and construct stout, tubular cases of coarse sand grains (Fig. 40.15K).

The family is restricted to the Australasian and Neotropical regions. About 9 genera and 20 species are known, of which 5 genera with 13 species occur in Australia.

**22. Odontoceridae.** Adults of Australian representatives are medium sized with wing span 14–20 mm; some robust, blackish species have stout antennae, others are slender, brownish with long filiform antennae. Ocelli absent. Maxillary palps 5-segmented in both sexes; segments long, cylindrical. Antennae as long as or considerably longer than fore wing, basal segment large. In males of some species the eyes are much enlarged and almost meet mesally (Fig. 40.6C). Mesoscutum either with pair of small, oval scutal warts or with 2 indistinct, longitudinal bands or groups of setiferous punctures; scutellum dome-shaped, rounded anteriorly, setal wart sometimes indistinctly outlined (Fig. 40.6B). Fore wings moderately broad to slender; discoidal cell closed, median cell absent; veins  $R_1$  and  $R_2$  frequently joined or connected by cross-vein near wing margin (Fig. 40.10I); venation sometimes irregular in males, differing from females. Tibial spurs 2:4:4 (Australian species).

Larval head usually carinate laterally, antennae at anterolateral margin of head capsule; fore trochantin small, simple apically; mesonotal sclerites clearly subdivided mid-dorsally, sometimes with transverse ridge; metanotum mostly membranous, with several paired, weakly-developed sclerites (Figs 40.14S–U). Abdominal segment 1 with dorsal and lateral spacing humps; abdom-

inal gills branched; anal claws curved, simple, usually without accessory hook; segment 8 with lateral row of small bifid spicules. The tubular cases are constructed of coarse sand grains, slightly curved, tapering posteriorly (Fig. 40.15J). The larvae are found in clear, cool-water streams.

The family is scattered throughout all faunal regions except Afrotropical; there are about 10 genera with 70 described species, of which 2 genera with 4 species are recorded from Australia; they are not known from Tas.

**23. Atriplectididae.** Adults of this family are slender, medium sized with wing span 20–28 mm; brown, with subdued mottled appearance and long, slender antennae; in general appearance not unlike some species of Triplectidinae (Leptoceridae). Ocelli absent. Maxillary palps (Fig. 40.10I) stout, 5-segmented and similar in both sexes. Antennae longer than fore wing, basal segment short, bulbous. Pronotal setal warts transversely elongate; mesoscutum with 2 longitudinal bands of setiferous punctures; scutellum with single mesal wart (Fig. 40.6D). Fore wings narrow, discoidal cell present, wing coupling with hamuli along anterior margin of hind wing (Fig. 40.10H). Tibial spurs 2:4:4.

Larval head (Figs 40.14B, C) narrow, elongate; ecdysial sutures not visible; antennae rather long, situated at anterolateral margin. Pronotum very slender with 2 pairs of dorsal sclerites anteriorly and long membranous retractile posterior portion; mesonotum wider than pronotum with 2 pairs of sclerites; metanotum with small median sclerite (Fig. 40.14A). Hind legs long. Abdominal gills filiform; segment 1 with dorsal spacing hump, lateral humps reduced; segment 8 with row of bifid spicules; claw of anal proleg with single accessory hook. Larval case tubular, slightly curved, constructed of sand grains, somewhat angular anteriorly. Larvae are found in bottom sediments of lakes and slow-flowing rivers.

The family is restricted to Australia and Seychelles Is, each with a monotypic genus. The Australian species is widely distributed in the eastern coastal regions (including Tas.), but in south-western Australia is restricted to a small, coastal area south of Perth.

**24. Calamoceratidae.** Adults (Fig. 40.1H) medium sized with wing span 15–26 mm, fore wings rather broad, somewhat triangular, densely covered with short, sometimes distinctly coloured hairs. Ocelli absent. Maxillary palps 6-segmented in both sexes (Australian species), long and densely covered with long erect hairs, apical segment simple (Fig. 40.10F). Antennae filiform, longer than fore wing, basal segment shorter than head, subsequent segments slender. Mesoscutum with setal warts replaced by 2 more or less distinct, irregular bands of setiferous punctures, mesal separation of bands often indistinct; scutellum small, squarish, without setal warts

Fig. 40.13 Larvae: A, *Tasimia* sp., Tasimiidae, head, dorsal; B, same, thoracic segments, dorsal; C, *Archaeophylax ochreus*, Limnephilidae, head, dorsal; D, same, head, ventral; E, same, thoracic segments, dorsal; F, *Tanjistomella verna*, Kokiriidae, fore leg; G, same, mid leg; H, same, hind leg; I, same, head, dorsal; J, same, thoracic segments, dorsal; K, *Tascuna ignota*, Oeconesidae, head, frontal; L, same, head, ventral; M, same, head and thoracic segments, dorsal; N, *Plectrotarsus gravenhorstii*, Plectrotarsidae, head, dorsal; O, same, head, ventral; P, same, thoracic segments, dorsal; Q, *Conoesucus* sp., Conoesucidae, head, dorsal; R, same, head, ventral; S, same, thoracic segments, dorsal; T, *Antipodoecia turneri*, Antipodoeciidae, head, ventral; U, same, head, dorsal; V, same, thoracic segments, dorsal; W, *Caenota plicata*, Calocidae, head, dorsal; X, same, head, ventral; Y, same, thoracic segments, dorsal.

[R. Plant, J. Dean]

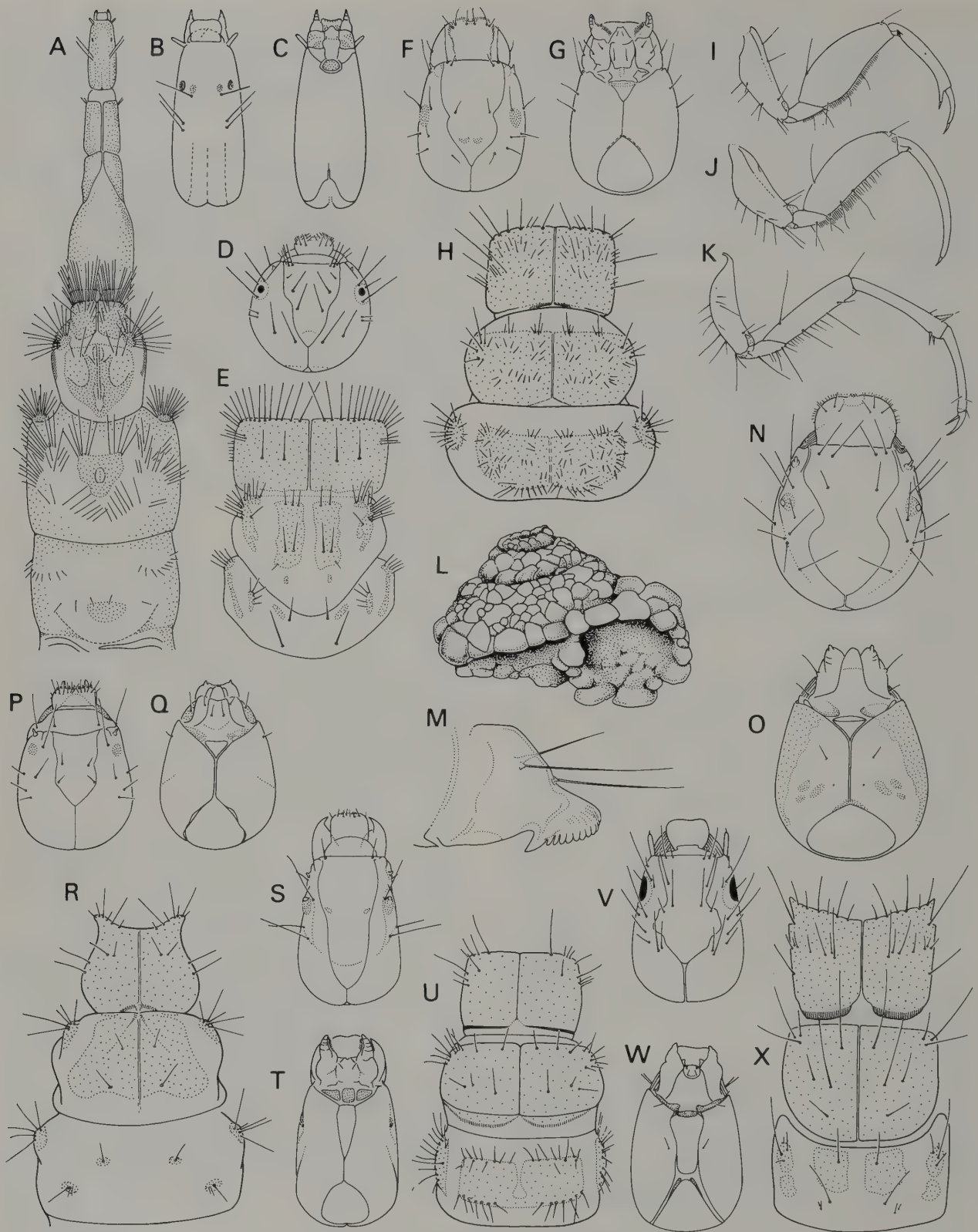


Fig. 40.14 Larvae: A, *Atriplectides dubius*, Atriplectididae, head and thoracic segments, dorsal (extended position); B, same, head, dorsal; C, same, head, ventral; D, *Alloecella grisea*, Helicophidae, head, dorsal; E, same, thoracic segments, dorsal; F, *Aphilorheithrus* sp., Philorheithridae, head, dorsal; G, same, head, ventral; H, same, thoracic segments, dorsal; I, same, fore leg; J, same, mid leg; K, same, hind leg; L, *Helicopsyche* sp., Helicopsychidae, larval case; M, same, abdominal proleg and claw, lateral; N, same, head, dorsal; O, same, head, ventral; P, *Anisocentropus bicoloratus*, Calamoceratidae, head, dorsal; Q, same, head, ventral; R, same, thoracic segments, dorsal; S, *Marilia* sp., Odontoceridae, head, dorsal; T, same, head, ventral; U, same, thoracic segments, dorsal; V, *Lectrides varians*, Leptoceridae, head, dorsal; W, same, head, ventral; X, same, thoracic segments, dorsal.

[R. Plant, A. Neboiss]



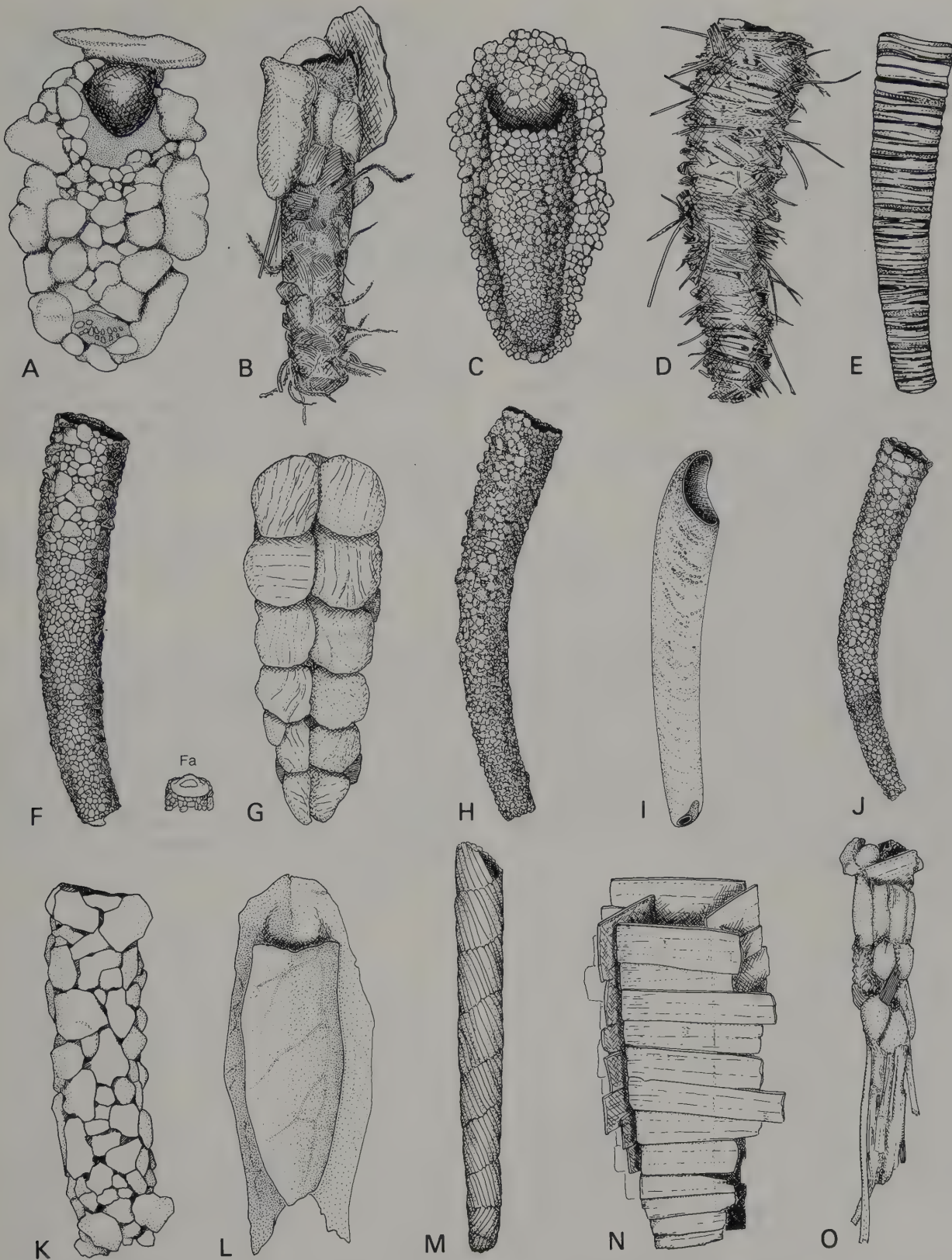


Fig. 40.15 Portable cases: A, *Tasimia* sp., Tasimiidae, ventral; B, *Tascuna ignota*, Oeconesidae; C, *Tanjistomella verna*, Kokiriidae, ventral; D, *Plectrotarsus gravenhorstii*, Plectrotarsidae; E, *Conoesucus* sp., Conoesucidae; F, *Antipodoecia turneri*, Antipodoeciidae, Fa, apical opening, ventral; G, *Caenota plicata*, Calocidae, dorsal; H, *Caloca saneva*, Calocidae; I, *Alloecella grisea*, Helicophidae; J, *Marilia* sp., Odontoceridae; K, *Austrheithrus* sp., Philorheithridae; L, *Anisocentropus* sp., Calamoceratidae; M, *Triaenodes volda*, Leptoceridae; N, *Oecetis* sp., Leptoceridae; O, *Condoceris paludosus*, Leptoceridae.  
[A. Neboiss]

(Fig. 40.6E). Fore wings broadly triangular, discoidal and median cells both present; venation usually similar in sexes with elongate, hyaline line between discoidal and median cells (Fig. 40.10G). Tibial spurs 2:4:3 (*Anisocentropus*).

Larval head with labrum bearing transverse band of approximately 16 setae (Figs 40.14P, Q). Pronotal sclerites with prominent anterolateral projections; mesonotal sclerite large, subdivided by median ecdysial line, antero-lateral sclerites small; metanotum with 3 pairs of small sclerites (Fig. 40.14R). Abdominal segment 1 with dorsal and lateral spacing humps; abdominal gills either single or branched; lateral fringe present; segment 8 with row of bifid spicules. Each larva constructs a dorsoventrally flattened tube-case from pieces of leaves (Fig. 40.15L), the upper and wider leaf completely obscuring the ventral part of the case as well as the apical opening. Larvae inhabit sluggish parts of rivers, lakes and swamps and feed on plant detritus.

The family, although represented in all faunal regions, is more common in the subtropics; it is known from 6 genera and about 100 species, of which only one genus with 10 species is recorded from Australia.

**25. Leptoceridae.** This family is easily recognised by long, slender wings and long filiform antennae (Fig. 40.11). Most are rather large with wing span 10–40 mm. Ocelli absent. Maxillary palps long, 5-segmented, apical segment incompletely sclerotised, flexible but not annulate, segment 2 longest. Antennae usually 2–3 times longer than fore wing, in males longer than in females; basal segment bulbous, rarely longer than head (Fig. 40.10M). Mesoscutum elongate, setal warts replaced by 2 longitudinal bands of setiferous punctures; scutellum small with few setiferous punctures (Fig. 40.6J). Fore wings long and narrow, discoidal cell closed, median cell absent; hind wings either narrow and acute apically, or considerably expanded (Figs 40.10K, N), sometimes with long fringe. Tibial spurs 0–2:2:2–4.

Larvae distinguished by slender legs with hind femur divided, and by long antennae (Fig. 40.14V), which are usually longer than 0.2 times width of anterior margin of frontoclypeal apotome and arise near base of mandibles, except in *Triplexa*, in which antennae minute, shorter than 0.2 times width of anterior margin and located about half way between eye and base of mandible; ventral apotome quadrate, and entirely separating genae (Fig. 40.14W) or, if triangular, genae not separated; mesonotal plates only lightly sclerotised, metanotum membranous or with sclerites (Fig. 40.14X); hind legs much longer than others. Abdominal segment 1 with dorsal and lateral spacing humps; abdominal gills single, branched or absent; lateral setal fringe usually present; segment 8 with row of bifid spicules. Larvae construct tubular cases (Figs 40.15M–O) of mineral and plant materials arranged in a great variety of ways; some use hollowed out pieces of wood or grass stems. Some larvae are omnivorous, others predatory. Habitats range from swift, mountain streams to temporary pools and saline lakes. Adults of some species are diurnal and can be seen flying along the water's edge among vegetation.

The family is very common and known from all faunal regions; there are 2 subfamilies—LEPTOCERINAE and TRIPLECTIDINAE with about 50 genera and more than 900 species; 14 genera and over 80 species of both subfamilies are known from Australia.

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# Lepidoptera

(*Moths and butterflies*)

E. S. NIELSEN and I. F. B. COMMON

Proboscis-bearing or rarely mandibulate, endopterygote Neoptera, without median ocellus, with two pairs of membranous wings clothed on both surfaces with usually overlapping scales. Larvae eruciform, peripneustic or rarely holopneustic. Pupae rarely decticious, usually adecticious and obtect.

The Lepidoptera is one of the largest insect orders, including some 10 000 described Australian species, with at least as many again still to be named. They range in size from tiny leaf-miners, with wings expanding barely 3 mm, to the huge hepialids, cossids and saturniids expanding some 25 cm. Their colouring and elegance have given them considerable popular appeal, while the destructive qualities of the larvae of many species establish the economic importance of the order.

Members of this order are readily distinguished from other panorpoid orders having two pairs of wings by the clothing of usually broad, overlapping scales on the head, body and appendages of the adult. The wing venation of the primitive homoneurous suborders approaches that of certain Trichoptera, but  $M_4$  rarely occurs as a separate vein terminating on the wing margin. An epiphysis is present on the fore tibia of most of these archaic Lepidoptera, as in all but a few of the more specialised families of the order, whereas this structure does not occur in other orders. The modification of the galeae into a proboscis (or haustellum), found widely in the Lepidoptera, occurs in no other order. Twenty-seven possible lepidopteran autapomorphies are listed by Kristensen (1984e).

## Anatomy of Adult

**Head** (Fig. 41.1). Compound eyes large, rounded, often with erect hairs between the facets; ocelli, when

present, paired, one above each eye; both sexes sometimes with paired sensory organs, *chaetosemata* (Jordan 1923; Fig. 41.1A). Epistomal or transclypeal sutures present in the most primitive groups, but frons not demarcated from clypeus in vast majority; genae narrow; labrum a narrow, pointed or transverse plate, usually with lateral projections (*pilifers*), often with setae, and a median projection. Corporotentorium with medial, posteriorly directed process. Antennae 3-segmented, usually partly clothed with scales, but sometimes naked; scape sometimes with tuft of scales, or with anterior pecten of stiff, hair-like scales, or laterally expanded and concave beneath forming an *eye-cap* (Fig. 41.22A); usually with intercalary sclerite between scape and pedicel; flagellum, usually of 20–60 units, in male more specialised than in female, varying greatly in structure, moniliform, filiform, ciliate, clubbed, dentate, serrate, lamellate or pectinate.

Mouth-parts (Fig. 41.1B) variable. Mandibles dentate (Zeugloptera, Heterobathmiina, Fig. 41.15B) or non-dentate (Aglossata, Fig. 41.15E), in both functional and furnished with well-developed abductor and adductor muscles. Mandibles functional only in pharate stage of most primitive families to move pupal mandibles at eclosion; vestigial in most Glossata. Maxillae with laciniae present and galeae not modified in Zeugloptera, Heterobathmiina and Aglossata (Figs 41.15C, F). In the Glossata laciniae rudimentary or absent and galeae often greatly elongated, usually grooved internally, and fastened

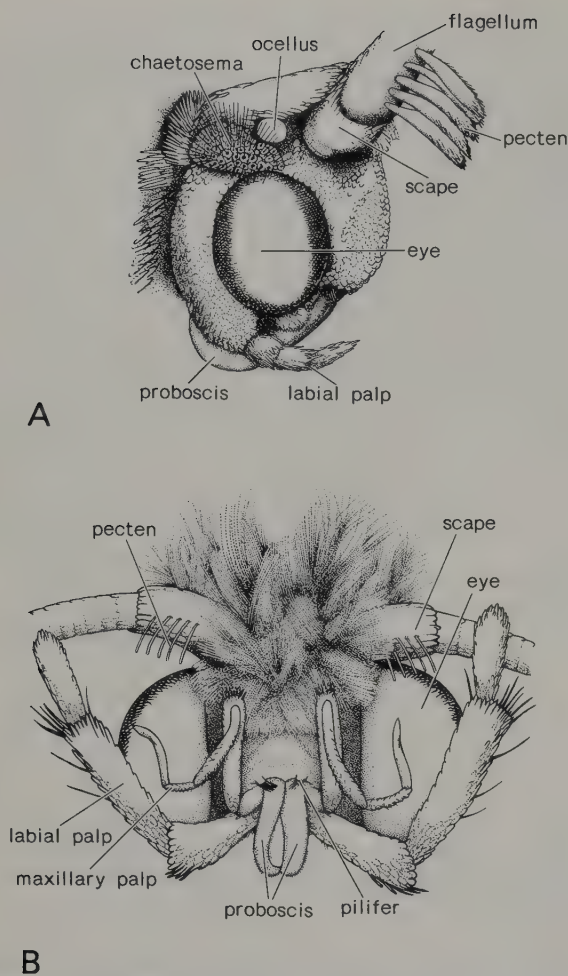


Fig. 41.1 Head and mouth-parts: A, *Pollanisis*, Zygaenidae, lateral; B, *Monopis*, Tineidae, ventral. [B. Rankin]

together by interlocking projections or spines to form a tubular *proboscis* (haustellum) through which liquid food may be drawn; the exotic Neopseustina have a pair of independent tubes; in most Lepidoptera the inner proboscis surfaces are covered with sclerotised plates and the two parts are joined together by a dorsal and ventral locking device, each half containing a nerve, a trachea and 2 sets of muscles which enable the proboscis to be coiled beneath the head when not in use; in most primitive forms the proboscis has only a single longitudinal muscle, or muscles are absent and coiling is due exclusively to wall elasticity. Proboscis often with dense, overlapping scales towards base and with prominent sensilla. Maxillary palps usually present and clothed with scales, often 5-segmented and folded in more primitive families, or reduced to 4, 3, 2 or 1 segment, or absent. Labium small, usually with well-developed, 3-segmented or rarely 2- or 1-segmented palps, clothed with scales, the apical segment bearing a usually invaginated sensory area (vom Rath's organ).

**Thorax** (Fig. 41.2). Prothorax usually small, often with a pair of stalked, dorsal protuberances, the *patagia*. Mesothorax large, with small prescutum, prominent scutum and smaller scutellum; *tegulae* uniformly well developed, each supported by a special subtegular plate of the notum and by a tegular arm invaginated from the base of the pleural wing process (Sharplin 1963–64). Metathorax only slightly smaller than mesothorax in primitive suborders, much smaller in the Heteroneura.

In Noctuoidea the metathorax carries a pair of auditory tympanal organs situated in cavities between the epimeron and the postnotum (Figs 41.6A, B; A. G. Richards 1983; H. G. Spangler 1988). The transparent and iridescent tympanic membrane, to the inner surface of which 1 or 2 chordotonal sensilla are attached, covers a large tracheal sac. The tympanum is usually separated from the membranous, posterodorsal portion of the epimeron by a small sclerite, the *epaulette* or nodular sclerite, which

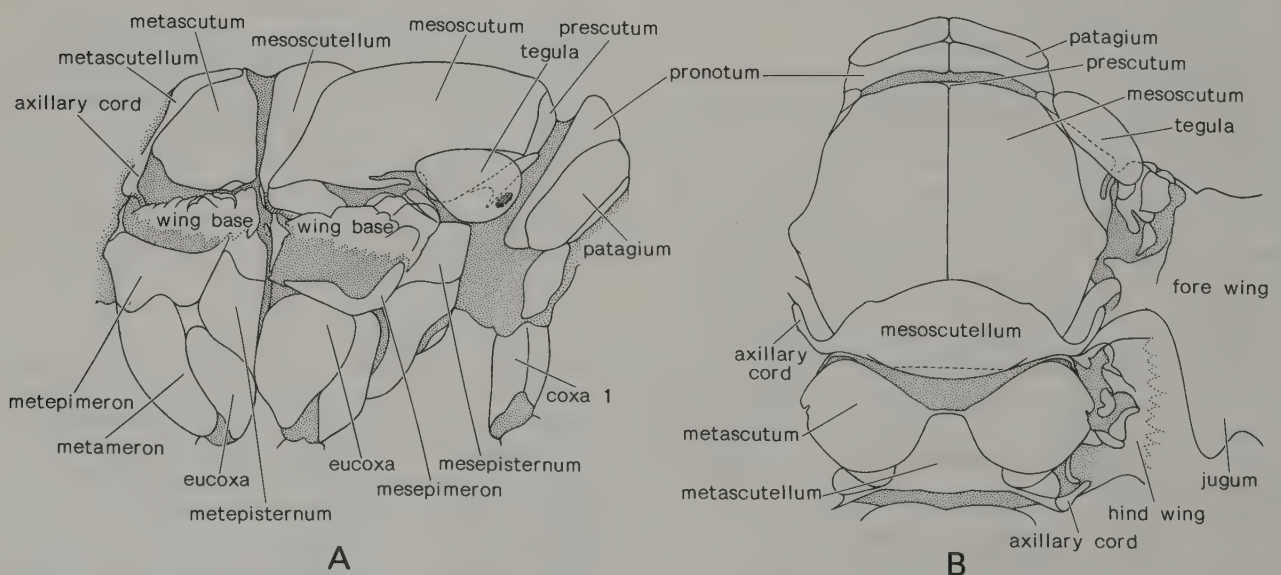


Fig. 41.2 Thorax of *Oncopera*, Hepialidae: A, lateral; B, dorsal. [B. Rankin]



varies greatly in shape between species. At the base of the abdomen, posterior to each tympanal cavity, there is usually a counter-tympanal cavity; a lateral *hood* covers the tympanal cavity posteriorly (Figs 41.6A, B).

**Legs** (Fig. 41.3). Usually well developed for walking and clothed with scales; fore legs reduced in some Papilionoidea, hind legs in some Hepialidae and Geometridae, all degenerate in females of some Psychidae. Pterothoracic coxae relatively immobile; trochanter small. Femur strong, often bearing long hairs. Fore tibia usually with leaf-like or spur-like, basally articulated *epiphysis* on inner surface, used for cleaning antennae or proboscis, sometimes with spines, bristles, long hairs or prominent scales; mid tibia usually with pair of apical articulating spurs; hind tibia usually with 2 pairs of spurs, one pair apical, the other medial; the number of spurs on the fore, mid and hind legs is shown conventionally by a formula (e.g. 0-2-4); males sometimes with expandable tuft or pencil of scent-scales on hind tibia, rarely on mid tibia. Tarsi 5-segmented, usually spined; apical segment with a pair of articulated, curved claws; claws simple, with a tooth (e.g. Drepanidae), bifid (Pieridae) or reduced; pretarsus usually with a median arolium and pseudempodium, and sometimes with well-developed lateral pulvilli (Fig. 41.3D).

**Wings.** Membranous; both surfaces usually clothed with 2 layers of overlapping, usually broad, flattened macrotrichia (*scales*) (Figs 41.4D, G), each with a short pedicel, inserted in a minute socket on wing membrane (Fig. 41.4A). *Normal-type scales* (Figs 41.4C, E, I) have an internal lumen with trabeculae and usually contain pigments, their upper surface bearing many fine, longitudinal ridges, transverse ridges (flutes) and perforations (windows). *Primitive-type scales* (Figs 41.4F, H) are solid and lack windows but have longitudinal ridges. Iridescent colours are due to scale structure. The most primitive Lepidoptera (Micropterigidae, Agathiphagidae, Heterobathmiidae, Eriocraniidae) possess only primitive-type

scales; most other non-ditrysians have a lower layer of primitive-type scales and an upper layer of normal-type scales; primitive-type scales are usually absent in Ditrysia. In males of some groups specialised scales (*androconia*), which disseminate scents secreted by associated glands, are scattered over wings, or in well-defined, sex brands, patches, tufts or pencils. Microtrichia or *aculei* (Fig. 41.4A) also present in most non-ditrysian suborders. The sides of the triangular lepidopterous wing are referred to as the *costa*, the *termen* (outer margin) and the *dorsum* (posterior margin or inner margin).

The wings in the females of a few Australian Cossidae, Psychidae, Oecophoridae, Geometridae, Anthelidae, Lymantriidae and Arctiidae are reduced and nonfunctional, or absent. On certain subantarctic islands brachyptery occurs in both sexes in several families.

**VENATION.** The most outstanding features are its simplicity and apparent uncompromising reduction from the homoneurous venation of the primitive suborders to the heteroneurous condition of the more advanced Lepidoptera.

The most generalised homoneurous venation of the Zeugloptera and the Aglossata (Fig. 41.14) closely resembles that of the more primitive Trichoptera. In both wings a humeral vein may be present, Sc and R<sub>1</sub> may each have 2 branches, Rs has 4 branches, M has 3 or rarely 4 branches, CuP is present, and the three anal veins are distally fused forming a double-Y configuration (anal loop or anal fork). Few cross-veins are retained. A homoneurous venation also occurs in the Heterobathmiina and in the infraorders Dacnonypha, Lophocoronina, Neopseustina and Exoporia of the Glossata.

The heteroneurous venation, found in the remainder of the Myoglossata (Nepticuloidea, Incurvarioidea, Palaeophatoidea, Tischerioidea and all Ditrysia) shows a trend towards simplicity produced by the fusion or loss of veins. The most generalised type of heteroneurous venation is retained in certain Cossidae (Fig. 41.48B), in which

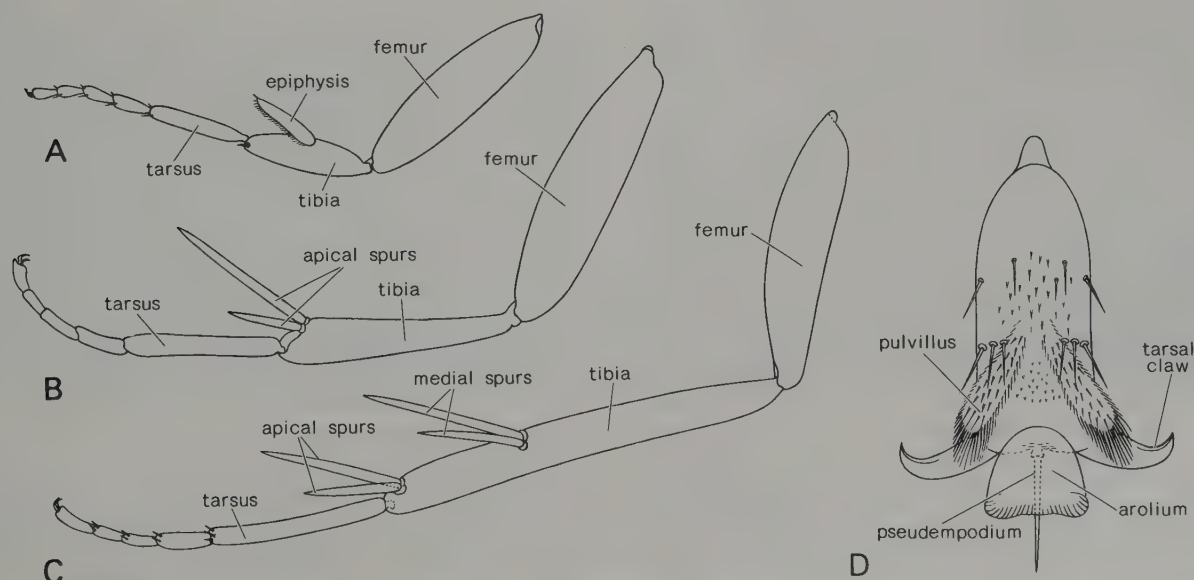


Fig. 41.3 Legs of *Epiphyas*, Tortricidae: A, fore; B, mid; C, hind; D, apical fore tarsal segment, ventral.

[B. Rankin]



the stem of  $R_{4+5}$  (*chorda*) forms an accessory cell in the fore wing, the stem of M is well developed and 2-branched, forming a second cell, and CuP is present in both wings. In the fore wing two anal veins are present but fused distally; in the hind wing Sc is fused, at least distally, with  $R_1$ ,  $R_s$  is unbranched, and three anal veins are present, although 1A and 2A practically coalesce. This venation is closely approached by some Psychidae (e.g. *Trigonocyttara*). The first step in reduction is the loss of the stem of M and the *chorda*, resulting in the formation of one large 'discal' cell. Further reduction varies between the superfamilies, but generally takes the form of

fusion or coalescence of the peripheral veins. In the fore wing one or two narrow accessory cells (*areoles*) may arise by the partial fusion of two or more radial veins. In the most advanced superfamilies CuP is absent in both fore and hind wing, but in the Tineoidea, Yponomeutoidea, Gelechioidea, Cossioidea, Tortricoidea, Castnioidea, Sesiioidea, Zygaenoidea, Immoidea and Copromorphoidea CuP has usually persisted, at least towards the wing margin.

**WING-COUPLING.** Coupling is effected in several different ways. In the homoneurous suborders a *jugum* projects from the inner margin of the fore wing (Figs 41.2B, 14,

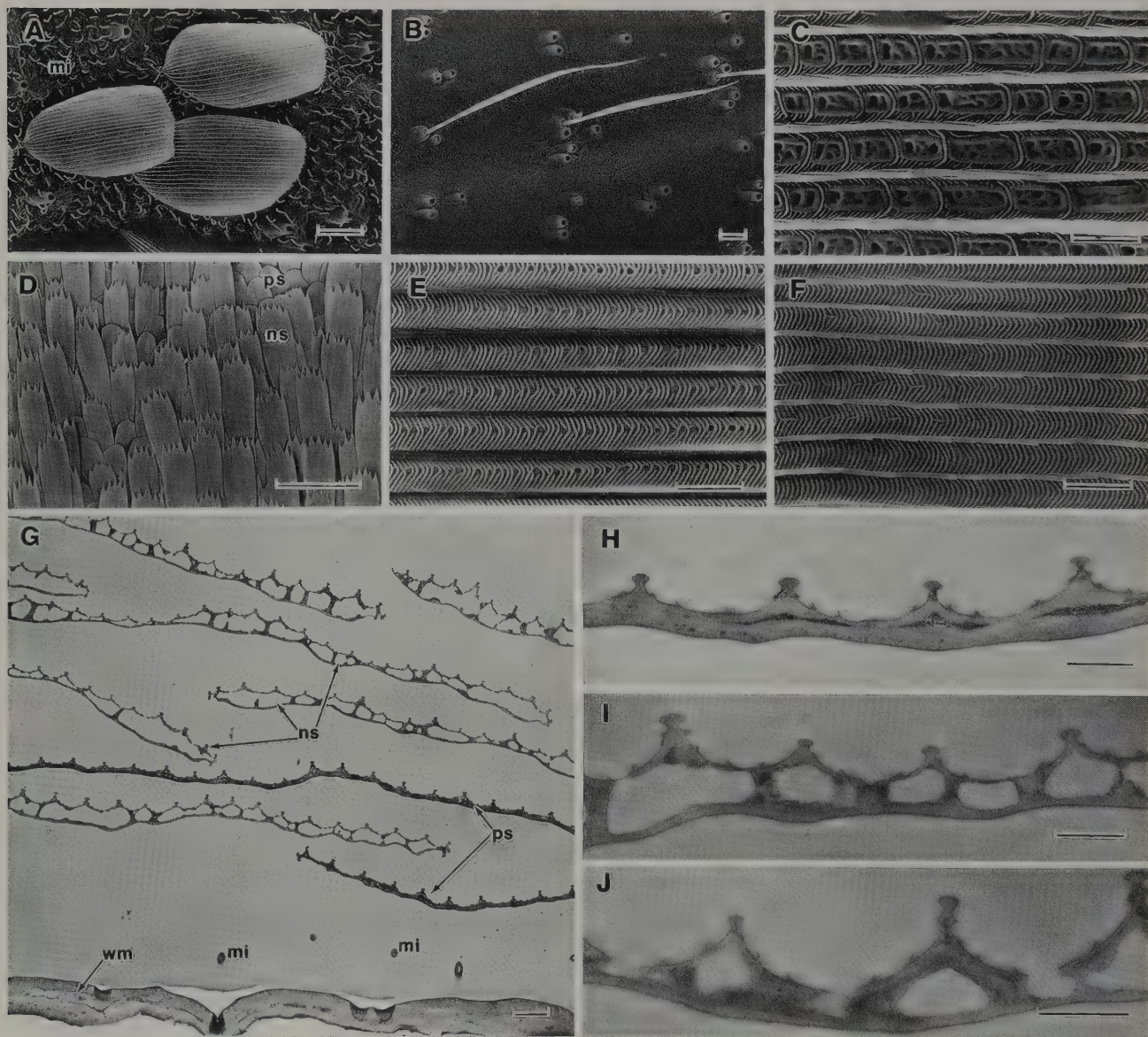


Fig. 41.4 Wing scales: A, D–J, *Tinea monophthalma*, ♂, Incurvariidae; B, *Monopis* sp., ♂, Tineidae; C, *Oncopera* sp., ♂, Hepialidae. A, upper wing surface with most scales removed, showing microtrichia and primitive-type scales; B, upper wing surface with all scales removed, showing sensory setae and absence of microtrichia; C, ultrastructure of normal-type scales, showing modified windows; D, scales on upper surface of fore wing, showing normal-type scales (long, with dentate apical edge) and primitive-type scales (broad, with rounded apical edge); E, surface of normal-type scales (note windows); F, surface of primitive-type scales (note absence of windows); G, cross-section of vestiture on upper surface of wing (note that normal-type scales form upper layer of scales); H, cross-section of primitive-type scales (note that scale is solid); I, J, cross-sections of normal-type scales (note that scales are lacunate). Scale lines: A, B = 10  $\mu$ m; C, E–G = 2  $\mu$ m; D = 100  $\mu$ m; H–J = 1  $\mu$ m.

[E. Brooks, K. Pickerd]

mi, microtrichia; ns, normal-type scales; ps, primitive-type scales; wm, wing membrane.



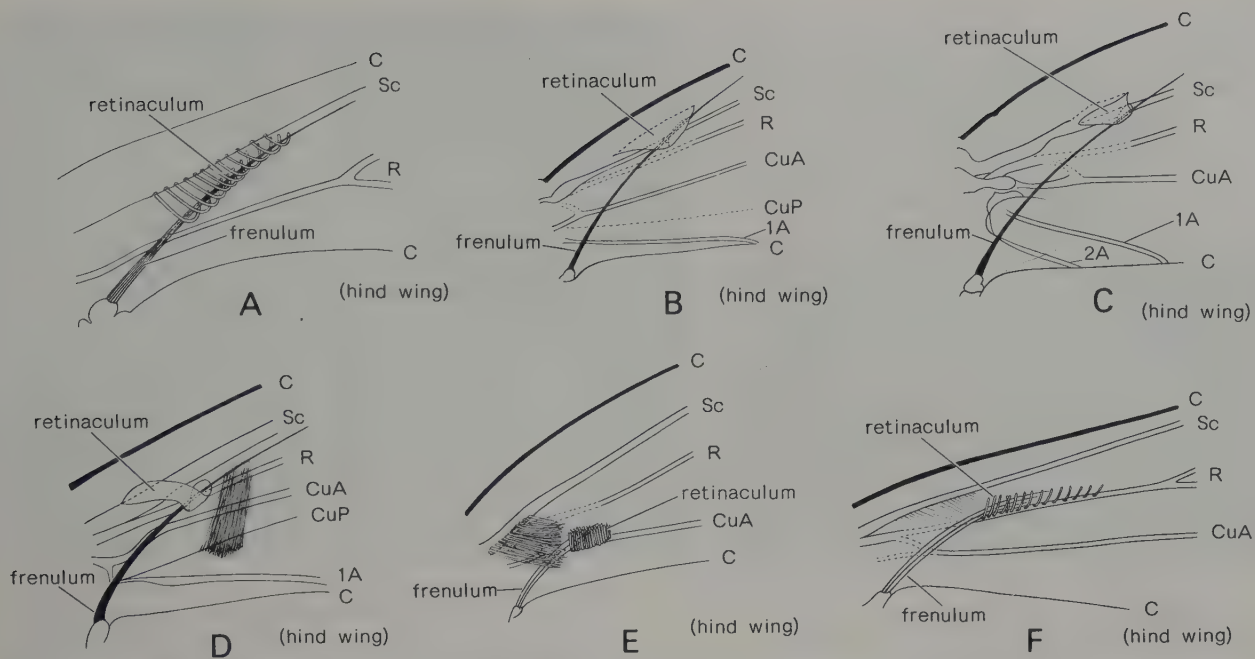


Fig. 41.5 Wing bases, ventral, showing retinaculum and frenulum: A, *Pectinivalva*, ♂, Nepticulidae; B, *Lepidoscia*, ♂, Psychidae; C, *Barea*, ♂, Oecophoridae; D, *Uresiphita*, ♂, Pyralidae; E, *Barea*, ♀, Oecophoridae; F, *Phthorimaea*, ♀, Gelechiidae. [B. Rankin]

19, 20) and lies above the base of the hind wing when the wings are extended, but folds beneath the fore wing when the wings are at rest. Sometimes a few small frenular bristles are also present, arising near the base of C of the hind wing, or a series of more distal costal bristles (*pseudofrenulum*) which press upon the anal area beneath the fore wing. Costal bristles are absent in Hepialidae, in some genera of which the jugum is long and thin.

A reduced jugum or jugal area persists in heteroneurous superfamilies up to and including the Pyraloidea (Sharplin 1963). In these forms, as in the rest of the Ditrysia, wing-coupling is effected by a true *frenulum* arising from a thickened frenulum-base at the humeral angle of the hind wing, and held beneath the fore wing by a *retinaculum* (Fig. 41.5). The frenulum is composed of a single, composite bristle in males and one to many bristles in females. In males, the retinaculum is a *subcostal* membranous hook, usually short and broad in the more primitive groups and arising between C and Sc, or on a spur of Sc, becoming narrow, more elongate, and arising on Sc in the more advanced forms. In females, it usually consists of one or two series of stiff, raised scales, arising near Sc (*subcostal*) or near CuA (*subcubital*), but occasionally R (*radial*); some males also have a subcubital retinaculum of hairs or scales near CuA. In the Nepticulidae and some Heliozelidae the retinaculum is a series of hooks arranged along the down-folded base of C (Fig. 41.5A), and in Opostegidae the wings are coupled by hooked pseudofrenular bristles which curve around an expanded vein of the fore wing. In some Nepticulidae, Incurvarioidea and Palaephatoidea pseudofrenular bristles may also be present. A few families of the Ditrysia, in which the frenulum is reduced or lost, feature the *amplexiform* method of wing-coupling. Here an enlargement of

the humeral area of the hind wing is substantially overlapped by the fore wing, and the former may then be strengthened by the development of one or more short humeral veins.

**Abdomen.** Segments 7–11 (of which 7–10 are more readily identified) may be greatly modified by the structures of the genitalia; S1 is lacking, except in a reduced form in most homoneurous groups. Functional spiracles on segments 1–7, rarely on 8. A pair of tympanal organs is found at the base of the abdomen (Fig. 41.6C), in *Harmaclona* (Tineidae), Dudgeoneidae, Pyraloidea, Geometroidea, Drepanoidea and females of Uranoidea and at the junction of segments 2 and 3 in males of Uranoidea. Tympanal-organ structure has been reviewed by Minet (1983). The dorsal surface of the abdomen in certain families of Yponomeutoidea, Gelechioidea, Alucitoidea and Sphingoidea bears scales which are modified into short, often flattened, spines. The anus in the male is situated at the end of an anal tube projecting behind segment 9, and in the female at the posterior extremity of the abdomen. Cerci are entirely lost. The abdomen may also contain eversible pheromone glands. Sex pheromone-producing glands, often eversible, are found in females of many families; the gland may be ring-shaped, dorsal, ventral or lateral, and is usually located on the intersegmental membrane between the genital segments (Percy-Cunningham and MacDonald 1987). Extrusible organs involved in courtship behaviour have been reported from various abdominal segments in males but are frequently associated with the genitalia (Birch and Hefetz 1987); hair-pencils associated with the male genitalia, *coremata*, are particularly common.

**Reproductive organs.** In both sexes of most Lepidoptera the genital organs provide characters of great value

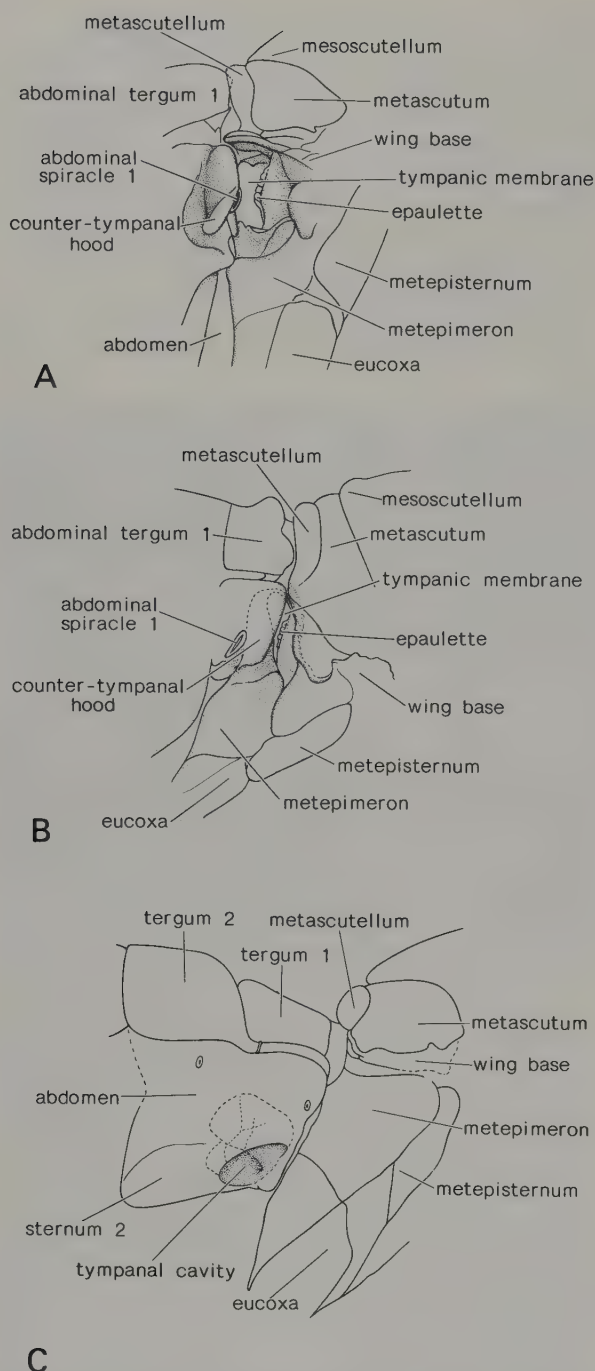


Fig. 41.6 Tympanal organs: A, *Agrotis*, Noctuidae, thoracic, showing postspiracular hood of counter-tympanal cavity; B, *Amsacta*, Arctiidae, thoracic, showing prespiracular hood of counter-tympanal cavity; C, *Chlorocoma*, Geometridae, abdominal. [B. Rankin]

in the separation of species, and often for the characterisation of genera and higher taxa. Their study normally necessitates the removal and dissection of the whole abdomen (G. S. Robinson 1976). The external genitalic structures are derived from the integument of abdominal segments 7 to 10. The internal genitalic structures, especially in the female, are also important. The homologies of the complex lepidopterous genitalia are not well under-

stood, even between some of the families within the order (Klots 1970).

**MALE** (Fig. 41.8). T9 and parts of T10 usually form a hood-like *tegumen*, from which arises various usually paired processes of the genitalia. Posteriorly, part of T10 forms a mid-dorsal *uncus*, which is usually simple and hook-like, but may be divided, modified or even absent. In certain groups T8 may bear an uncus-like process. Ventrally, S9 forms a U-shaped *vinculum*, the upper ends of which articulate with the ventral extremities of the tegumen. Midventrally, the vinculum may be produced anteriorly within the body cavity to form paired or unpaired apodemes (*saccus*). In some families paired, lightly sclerotised, often hairy *socii* arise from the posterior margin of the tegumen, beneath the uncus. Adjacent to the socii, a pair of processes derived from S10 articulates with the posterior margin of the tegumen; these together form the *gnathos* and are often fused medially. The anal tube (probably largely formed by segment 11), projecting between the gnathos and the ventral surface of the tegumen and uncus, may also be variously sclerotised.

The posterior end of the abdomen is closed by a membranous *diaphragma*, through which the *aedeagus* projects. Sclerotised portions of the diaphragma above, beneath and around the aedeagus are called respectively the *fultura superior*, the *fultura inferior* and the *anellus*. The fultura superior at times takes the form of a transverse band (*transtillia*), while the fultura inferior may form a sclerotised plate (*juxta*) to which the aedeagus may be hinged or fused. The invaginated distal end of the aedeagus forms an inner tube (endophallus) known as the *vesica*, which is everted during copulation and penetrates the female bursa copulatrix. The exterior of the everted vesica often bears sclerotised areas or spines, which may be shed in the bursa copulatrix. The paired clasping organs (*valvae*) usually articulate with the tegumen and vinculum, and may be derived from the coxites, styli or parandrites of segment 9. Each valva is a flattened sac, open proximally, and may be simple and rounded, or may assume a complicated shape and bear a variety of often complex structures and spines.

The testes lie adjacent to the intestine just beneath T5 and T6. Each usually consists of 4 follicles (in Adelidae 20). The follicles are normally compressed together, but occasionally (Agathiphagidae, some Hepialidae) they remain separate. The two testes are either separate from one another, each contained in a separate 'scrotum' (Zeugloptera, some Bombycoidea, some Papilionoidea), or, more usually, fused and contained in a common 'scrotum'. Each slender *vas deferens* opens into a *ductus ejaculatorius*, the pair uniting to form a single duct leading to the aedeagus. Spermatozoa are stored both in dilations (which may not all be homologous) of the vasa deferentia, the *vesiculae seminales*, and in the ductus ejaculatorius duplex. The latter also stores the secretion from one, rarely two, pairs of tubular *accessory glands* which join them. This secretion provides a medium for the spermatozoa in the spermatophore, and also initiates peristaltic contractions in the muscles of the female ductus seminalis. The simple distal ductus ejaculatorius includes



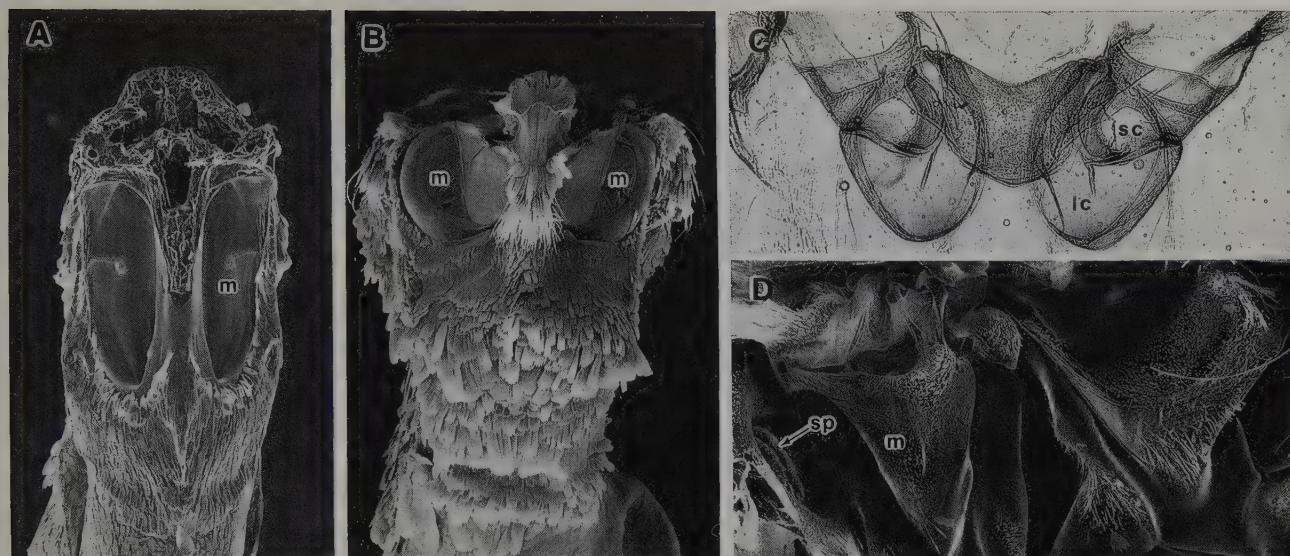


Fig. 41.7 Tympanal organs: A, *Harmaclona*, Tineidae, abdominal; B, *Epipaschiinae*, Pyralidae, abdominal; C, *Hypsidia*, Drepanidae, abdominal; D, *Destolmia*, Notodontidae, thoracic.

lc, large tympanal chamber; m, membrane; sc, small tympanal chamber; sp, spiracle.

two secretory sections in which the spermatophore is produced. In many Lepidoptera the spermatophore may disintegrate soon after deposition in the female genital tract, but in some groups, such as Noctuidae, it is very durable and contains chitin (Callahan and Cascio 1963).

**FEMALE.** Two main types of genitalia (Fig. 41.9), the *monotrysian* and the *ditrysian*, are found in female Lepidoptera. Except for the Exoporia, the monotrysian type occurs throughout the homoneurous groups, together with the Nepticuloidea, Incurvarioidea, Palaephatoidea and Tischerioidea. The ditrysian type is found throughout the Ditrysia. The *exoporian* type (see below) is confined to the Exoporia (Dugdale 1974).

The external genital aperture (*ovipore*) is situated on the fused segments 9–11 at the posterior extremity of the

abdomen. It is usually flanked by a pair of soft, hairy lobes, the *papillae anales*, but these may be heavily sclerotised and modified for the insertion of the eggs into plant tissues or into crevices, and the terminal segments of the abdomen may be extensible and serve as an ovipositor. The muscles operating the terminal segments of the female abdomen are inserted on paired, sclerotised apodemes, which extend forward from segment 8 (*apophyses anteriores*) and from the bases of the papillae anales on segment 9–10 (*apophyses posteriores*). In monotrysian genitalia (Fig. 41.9A) a single, terminal genital opening serves for both copulation and oviposition. In ditrysian genitalia (Figs 41.9B, C) an additional copulatory opening, the *ostium bursae*, is situated mid-ventrally on S7 or S8, or between S7 and S8. Exoporian genitalia,

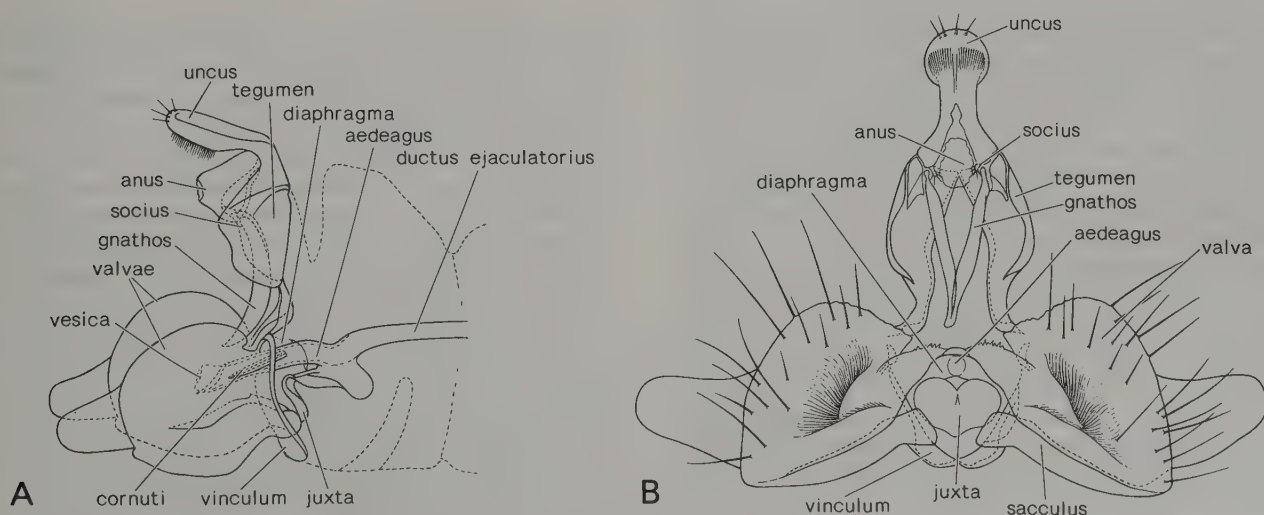


Fig. 41.8 Male genitalia of *Epiphyas*, Tortricidae: A, lateral, B, posteroventral.

[B. Rankin]

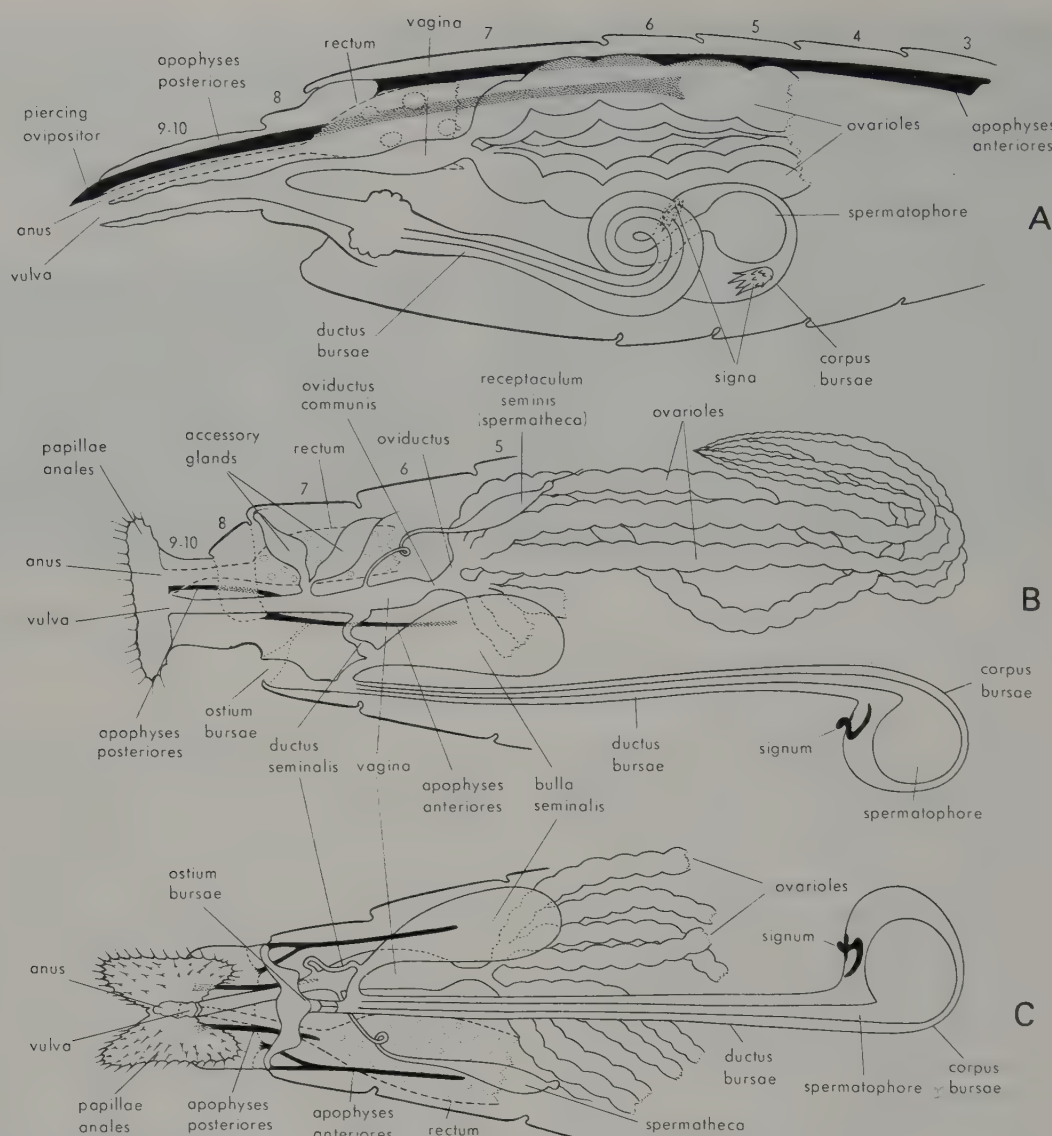


Fig. 41.9 Female genitalia, diagrammatic: A, monitryian type, lateral; B, ditryian type, lateral; C, ditryian type, ventral.

[B. Rankin]

found in the Hepialoidea and Mnesarchaeoidea, also have a separate copulatory opening, but this is situated close to the terminal genital opening on segment 9–10.

In most female Lepidoptera each ovary has 4 polytrophic ovarioles, but up to 20 are known in a few Incurvarioidea and Sesiidae and 45 in Agathipagidae. The egg passes from the ovary through an *oviductus* to the *oviductus communis*, and thence to the invaginated genital chamber (*vagina*), the anterior part of which is often enlarged and termed the *vestibulum*. The egg is fertilised in the vagina before passing to the ovipore. At copulation the spermatozoa, contained in a spermatophore, are received into an elongate sac, the *bursa copulatrix*. From there they may pass direct to the vagina (monitryian genitalia), or through a lateral duct, the *ductus seminalis*, to the vestibulum and thence to the *receptaculum seminis* or *spermatheca*, where they are stored before finally returning to the vagina to fertilise the ova (ditry-

sian genitalia). In exoporian genitalia the spermatozoa pass out from the external opening of the bursa copulatrix, the ostium bursae, along a mid-ventral groove to enter the vagina through the genital aperture.

Three sections of the bursa copulatrix are recognised, the *ostium*, *ductus* and *corpus bursae*. The ostium bursae is often surrounded by a sclerotised area (*sterigma*), which is sometimes formed into a projecting tube. The ductus bursae and the corpus bursae may be membranous or variously sclerotised, and the inner wall of the corpus bursae frequently bears one or more sclerotised *signa*, usually in the form of spines or of dentate or roughened patches. In the Ditrysia the orifice of the spermatophore approximates the point in the corpus bursae or ductus bursae from which the ductus seminalis leads to the vestibulum. Before reaching the vestibulum the spermatozoa are sometimes stored temporarily in a diverticulum of the ductus seminalis, the *bulla seminalis*. Paired accessory



glands open by a common duct into the roof of the vagina. Their secretion is used as an adhesive or covering for the eggs, but may also serve as a medium for the motile passage of the spermatozoa across the vagina to the spermatheca (Callahan and Cascio 1963). In Hepialidae, which scatter their eggs, accessory glands are absent.

**Internal Anatomy.** In adult Lepidoptera with a functional proboscis, liquids pass through it to the sucking pump, where a partial vacuum is created by muscular dilation. By contraction of the pharynx, the liquid continues its passage backwards into the long slender oesophagus. Posteriorly the oesophagus is usually dilated to form a crop. The crop may be a symmetrical dilation (Hepialidae, Cossidae, some Psychidae, some Tineidae), a lateral dilation (some Tineidae, Zygaenidae) or a diverticulum connected to the oesophagus by a short, narrow duct (most Lepidoptera). A tubular, chitinous peritrophic membrane occurs in the mid gut of several families (D. F. Waterhouse 1953). Usually 6 Malpighian tubules, singly (in a few primitive taxa) or in two groups of 3, enter at either side of the anterior end of the hind gut through a pair of chambers. They are reduced to 2 in *Tineola*, *Monopis* and *Galleria*. The central nervous system of the adult contains fewer ganglia than that of the larva. In the Hepialidae there are 3 thoracic and 6 abdominal ganglia; 5 abdominal ganglionic masses occur in the Agathiphagidae, 3 in some Micropterigidae, Nepticulidae and some Eriocraniidae and as few as 2 are present in some Micropterigidae and Opostegidae; as many as 7 abdominal ganglia are found in some psychid females; in the remainder the ganglia of the meso- and metathorax are fused, and there are 4 abdominal ganglia. The reproductive system has been described above. Kristensen (1984a) described the respiratory system of a micropterigid.

Recent accounts of the morphology and anatomy of adult lepidopterans are given by D. R. Davis (1986) on Palaephatidae, Eaton (1988) on a sphingid, Nielsen and Kristensen (1989) on hepialids, Oseto and Helms (1976) on a noctuid and Sorensen (1980) on a lycaenid butterfly.

### Immature Stages

**Egg.** Two types of egg may be distinguished in the Lepidoptera: a *flat* type and an *upright* type. The flat egg is asymmetrical in horizontal section, the micropylar axis is usually horizontal, and the micropyle is at one end. The upright egg is symmetrical in horizontal section, the micropylar axis is vertical, and the micropyle is at the top. The chorion may be relatively smooth, it may bear a regular or irregular sculptured pattern, or, as in most eggs, especially in the upright type, prominent ribs, usually with cross-ribbing as well. The micropyle is often surrounded by a rosette-like pattern of radiating ribs (Hinton 1981; Fehrenbach *et al.* 1987).

**Larva.** The larva, or caterpillar, exhibits a clear division into head, thorax and abdomen (with 10 discernible segments). Both hypognathous and prognathous forms occur, depending to a large extent upon their feeding behaviour.

The head (Figs 41.10A–C) is a heavily sclerotised capsule with a very large occipital foramen, and is usually

strengthened dorsally by an inverted Y-shaped internal ridge, represented on the dorsal surface by median and lateral *adfrontal* sutures (Hinton 1947a). Laterally, beyond the adfrontal sutures, there is usually a pair of ecdysial lines, which represent the dorsal lines of cleavage at ecdysis and normally appear only in late or last instars. The triangular area between the lateral adfrontal sutures is a composite frontoclypeus, bordered laterally by the two adfrontal areas. Anterior to the frontoclypeus is the *anteclypeus*, articulating with which is the labrum. The mandibles are normally well developed and dentate, but are modified in the sap-feeding instars of leaf-miners. The maxillae usually have well differentiated cardo and stipes and 3-segmented palps (Grimes and Neunzig 1986a, b). The submentum, mentum and prementum can be distinguished in the labium, the last usually carrying a median *spinneret* and a pair of minute, lateral, usually 2-segmented palps. The antennae are usually short, 3-segmented, and bear several sensilla (Dethier 1941). They are usually situated lateral to the anterior extremity of the adfrontal sutures. Posterior to the antenna is a group of usually 6 (7 in Heterobathmiina) stemmata which may be reduced in number or be absent. Randriamamonjy (1963) gives a detailed account of the anatomy of a larval head.

Each thoracic segment bears a pair of 5-segmented legs, terminating in a single claw. Occasionally they are modified, reduced or lost. The prothorax carries a large, dorsal, sclerotised area (*prothoracic shield*) and a pair of lateral spiracles.

Spiracles usually occur also on segments 1 to 8 of the abdomen. Leg-like processes (*prolegs*) are usually borne on segments 3 to 6 (*ventral prolegs*) and on 10 (*anal prolegs*). The truncate end of each proleg, the *planta*, usually bears small, sclerotised hooks or *crochets*, the form and arrangement of which are of taxonomic importance (Figs 41.10D–I). The crochets may be all of one length (*uniordinal*), of two or three alternating lengths (*bi-* or *triordinal*) or of many lengths (*multiordinal*). In the more primitive families they are usually arranged in a complete circle or ellipse, sometimes in two or more series; or the circle may be broken on the inner side (*lateral penellipse*) or on the outer side (*mesal penellipse*). Occasionally they are arranged in one or two transverse bands, and in the more specialised arboreal larvae in a longitudinal median row (*mesoserries*), the outer crochets of each circle having been reduced or lost, or in a combined mesoserries and reduced *lateroserries*. The prolegs may be reduced in size or number and, especially in some of the leaf-miners, may be lost altogether.

The head and body of the larva bear *setae* and *punctures* (probably campaniform sensilla). *Primary* setae or punctures are almost invariably present in the 1st instar, and are fairly constant in number and distribution. A few *subprimary* setae, also with definite positions, appear in the 2nd and later instars. The primary setae are mostly long and tactile in function, but there are a few *microscopic* primary setae, thought to be proprioceptors. These occur near the anterior margin of each segment, near the posterior margin of the prothorax and along the posterior margin of the head capsule. In many families, especially

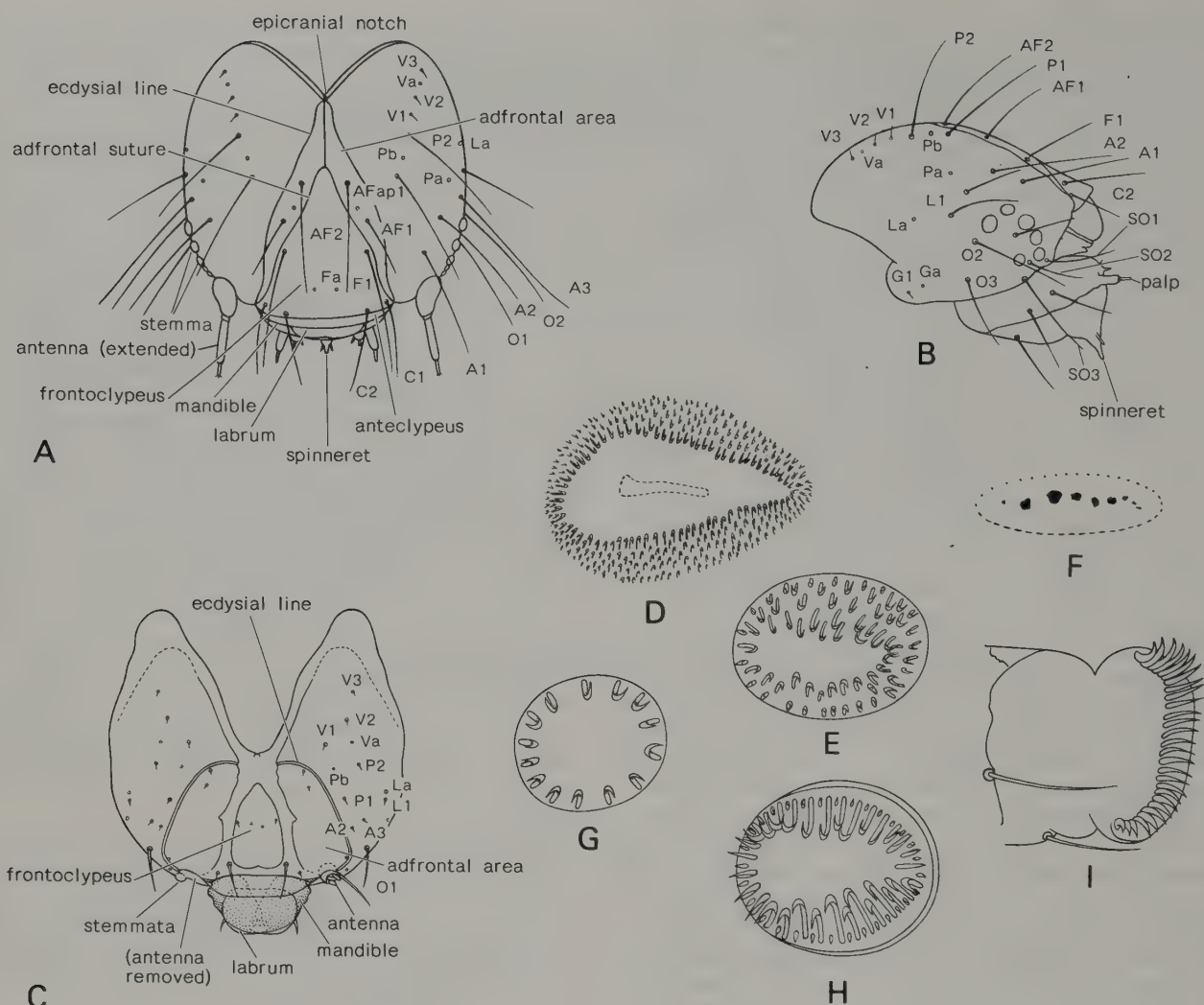


Fig. 41.10 Larvae: A, B, head of *Epiphyas*, Tortricidae, dorsal and lateral; C, head of *Eriocrania*, Eriocraniidae; D–I, arrangement of crochets: D, multiserial (Hepialidae); E, multiserial (Yponomeutidae); F, transverse band (Incurvariidae); G, uniordinal circle (Carposinidae); H, triordinal circle (Pyrilidae); I, uniordinal meseries (Noctuidae). [B. Rankin]

those with concealed larvae, further setae are not acquired. In others much more generally distributed *secondary* setae appear, and may form tufts or pencils, which may be grouped on sclerotised plates or various elevations and processes of the body wall (e.g. *scoli*); they are sometimes found even on the mandibles. In some families, such as the Arctiidae, the primary setae are replaced by *verrucae*, tufts of secondary setae borne on raised plates. In others, such as the Lymantriidae, secondary setae are present in the first instar obscuring the primary setae, and later pencils of setae borne on flat plates (*verricules*) may be present.

Pioneering work on the homology of larval setae has been done by a series of workers, notably by Fracker (1915). The most generally adopted nomenclature (Table 41.1) is that proposed by Hinton (1946a) and Hasenfuss (1963) has provided a comparative study of setal patterns. The setal patterns (chaetotaxy) are used widely for the identification of larvae and contribute information used in

the higher classification of the Lepidoptera (Stehr 1987b; D. J. Carter 1987). The distribution of the setae on each segment is usually plotted on a rectangular setal map, which represents the flattened integument extending from the mid-dorsal to the mid-ventral lines (Fig. 41.11).

**INTERNAL ANATOMY.** The alimentary canal of the lepidopterous larva is a relatively simple tube with few convolutions. The oesophagus is short, rarely with a diverticulum, the mid gut seldom has caeca or diverticula, and the hind gut is very short. A peritrophic membrane is present in the mid gut. Normally 6 Malpighian tubules, in two groups of 3, open proximally on either side into a small excretory chamber leading to the hind gut. Paired labial silk glands, homologous with the salivary glands in other insects, lead through a common duct to the spinneret, within which lies the spinning apparatus. Paired accessory glands usually open into the silk ducts near their anterior end. The tube-like silk glands are often extremely long, especially in the Bombycoidea. Paired



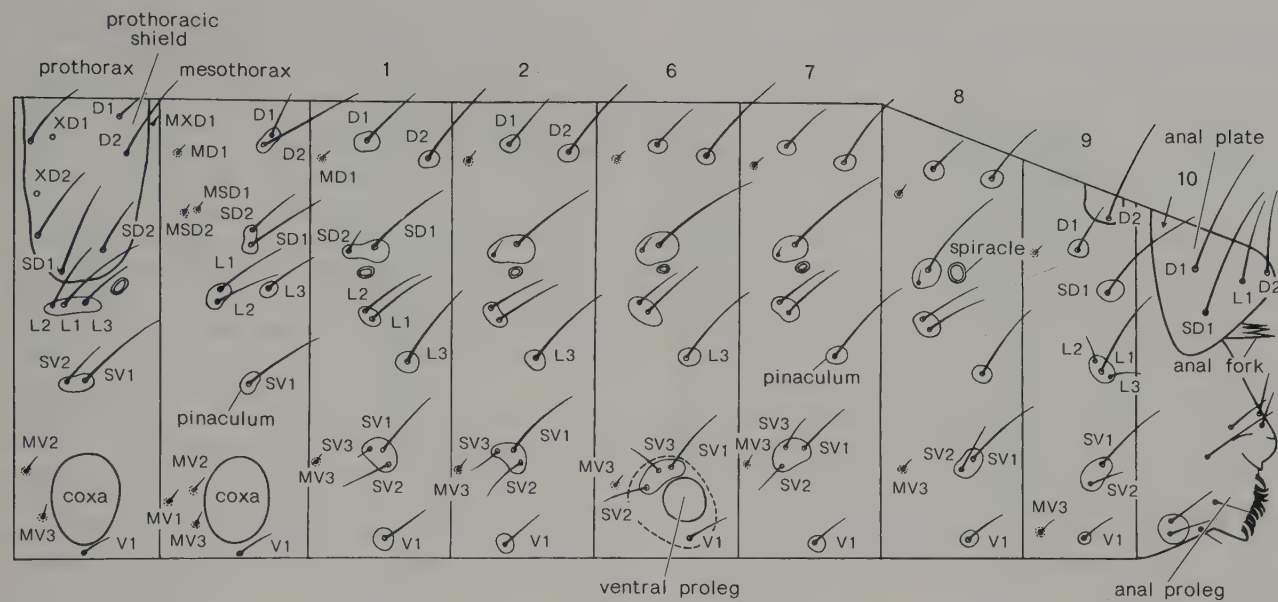


Fig. 41.11 Setal map of larva of *Epiphyas*, Tortricidae. [B. Rankin]

mandibular glands, which function as salivary glands, usually open on the inner side of each mandible near the base. The central nervous system consists of the brain, suboesophageal ganglion, 3 thoracic ganglia joined by paired connectives, and 7 or 8 abdominal ganglia joined by single (fused) connectives. The gonads are situated in abdominal segments 5 or 6, on each side of the dorsal vessel, and are visible through the integument in male larvae of many less advanced families.

**Pupa.** The term pupa is used in this chapter in the conventional sense. It refers to the entire insect from the time the last larval skin was shed until the shedding of the pupal cuticle by the emerging adult. The most extensive study of lepidopterous pupae is that of Mosher (1916). The various components of a pupa are demarcated by sutures (Fig. 41.12), some of which may be lacking in the more specialised families. The head, thorax and abdomen can be distinguished readily. In the

Table 41.1 Nomenclature and usual distribution of the setae of the thorax and abdomen in larvae of Lepidoptera (Hinton 1946a).

Tactile Setae	Thorax			Abdomen
	I	II	III	1–9
XD1	+	–	–	–
XD2	+	–	–	–
D1	+	+	+	+
D2	+	+	+	+
SD1	+	+	+	+
SD2	+	+	+	+ <sup>1</sup>
L1	+	+	+	+
L2	+	+	+	+ <sup>2</sup>
L3	+	+	+	+ <sup>2</sup>
SV1	+	+	+	+
SV2	+	±	±	±
SV3	–	–	–	± <sup>3</sup>
V1	+	+	+	+
Microscopic or Proprioceptors				
MXD1	±	–	–	–
MD1	–	+	+	+
MD2	–	–	±	±
MSD1	–	+	+	–
MSD2	–	+	+	–
MV1	–	+	+	–
MV2	+	+	+	–
MV3	+	+	+	+

<sup>1</sup>Always absent on 9.   <sup>2</sup>Often absent on 9.   <sup>3</sup>Always absent on 8 and 9.

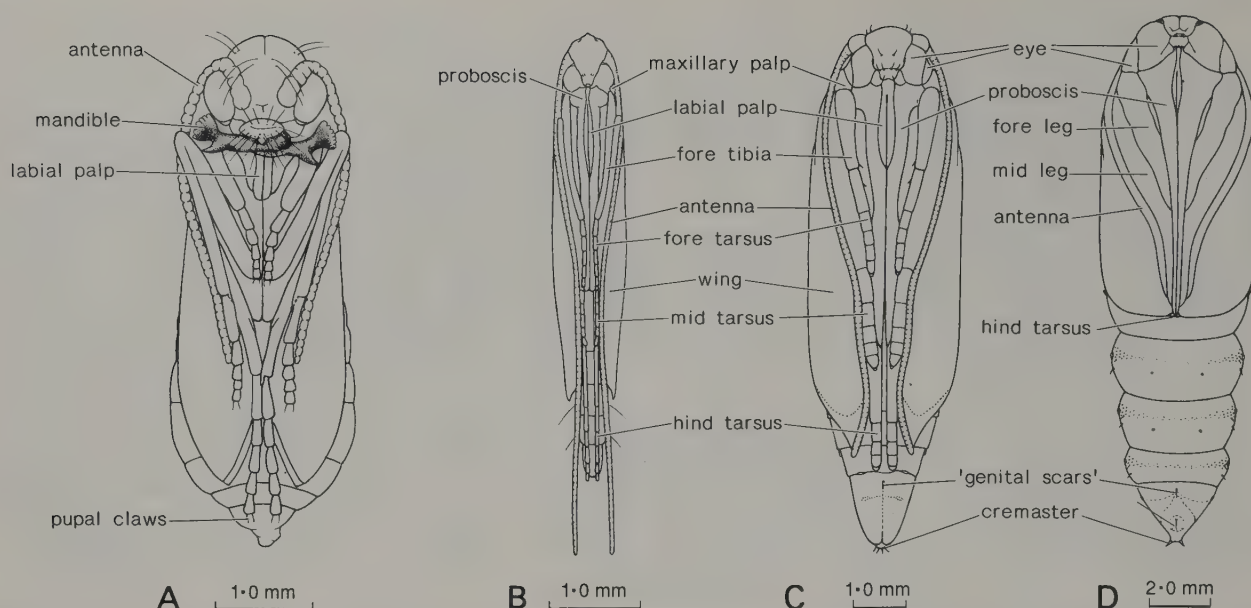


Fig. 41.12 Pupae, ventral: A, dectitious, exarate (*Agathiphaga*, Agathiphagidae); B–D, aedeuctitious, obect: B, *Acrocercops*, Gracillariidae; C, *Yponomeuta*, Yponomeutidae; D, *Persectania*, Noctuidae. [A by I. F. B. Common; B–D by B. Rankin]

head the frontoclypeal and clypeolabral sutures are usually not distinct. Posterolateral projections of the labrum, the *pilifers*, are recognisable in a few Yponomeutoidea, most Pyraloidea, and in Pterophoroidea, Hesperioidea and Papilionoidea. Functional mandibles are found only in the Zeugloptera, Aglossata, Heterobathmiina and the earliest Glossata (pupae decticae), and are operated by the muscles of the pharate adult to cut open the cocoon or to assist escape (Fig. 41.12A). These are hypertrophied and dentate in the last three groups. Small, non-functional mandibles, adjacent to the posterolateral angles of the labrum, are present in the pupae of many families (pupae aedeucticae). Maxillary palps are frequently present near the posterior margin of the eyes. The labial palps are often visible, but may be concealed by the proboscis. The head of the pupa sometimes bears a pointed projection which aids its escape from the cocoon.

The three thoracic segments are visible dorsally, and are of nearly equal length in the generalised species; in the remainder, the mesothorax is the longest. One pair of spiracles is visible, between pro- and mesothorax. Primitive forms have exarate pupae, whereas the appendages are glued to each other and to the body to various degrees in the obect pupae of more specialised forms. In some species with brachypterous females the wings of the female pupa show little reduction, but in *Orgyia* and the more specialised Psychidae they are greatly reduced.

Of the 10 abdominal segments, independent movement is never possible in the last 3. The number of free or movable segments is greatest in the most primitive forms. Segments 1 to 7 are free in the Zeugloptera, Aglossata, Heterobathmiina, Glossata and Nepticuloidea, and 2 to 7 or 2 to 6 in the Exoporia and in some of the lower Ditrysia. The male usually has one more movable seg-

ment than the female. In the higher Ditrysia only 3, or even fewer, abdominal segments are movable. Pupae with more than 3 movable segments are sometimes known as 'pupae incompletae'. Segments 1–8 of the abdomen have spiracles, but those on 1 are seldom visible, and those on 8 are non-functional. Segment 10 is sometimes modified to form the *cremaster*, which may bear a series of usually hooked setae used to attach the pupa; the cremaster is seldom present in the more generalised forms. Segment 10 also bears a circular or slit-like 'scar' which represents the anus. The genital openings of the ditrysid adult are represented by 'scars' on S9 in the male and usually on S8 and S9 in the female. The mobile abdomen of more primitive pupae is often armed with backwardly directed dorsal spines, which force the pupa forward when the abdomen is wriggled. These pupae partially emerge from the cocoon or larval shelter just before ecdysis. In the more advanced forms ecdysis occurs within the cocoon or shelter, and adult emergence is facilitated in various ways. The cocoon often has a weak area, or a slit-like or funnel-like opening at one end, which permits the adult to escape easily (e.g. *Anthela*). The newly emerged adult sometimes regurgitates a fluid which softens the silk (*Cerura*), and sometimes cuts a hole through the softened silk by means of a sharp hook on the 1st axillary sclerite of the fore wing (*Opodiphthera*).

### Biology

The remarkable success of the Lepidoptera seems to have been associated directly with the development of the higher plants, especially the angiosperms, in the Upper Cretaceous and Tertiary. A predominantly phytophagous group, it has demonstrated its great plasticity and adaptability in exploiting most parts of the plant.

**Adults.** The evolution of the proboscis probably con-



tributed substantially to the success of the Lepidoptera. Not only did it enable the adults to ingest water freely, thus increasing their resistance to desiccation, but it also permitted utilisation of the carbohydrates or other nutrients contained in nectar, which the lepidopteran can convert to, and store as, fat. In some species carbohydrate food is essential before egg maturation can ensue; in others it greatly increases egg output; in most it increases longevity. Sometimes the ingestion of carbohydrates is necessary before mating can occur. On the other hand, feeding is often not possible in forms with greatly reduced mouth-parts, and the eggs are ready for deposition when the adult sheds the pupal cuticle.

At rest the wings are folded in a variety of ways. The ancestral method of folding the wings roofwise above the abdomen, with the hind wing covered by the fore wing (Fig. 41.35), is characteristic of most moths. The slope of the fore wing in such species varies from almost vertical to almost horizontal. Many exceptions to this resting position may be noted. In many Geometridae and some other groups, the wings are expanded flat, and appressed to the substrate; in most Papilionoidea they are held back to back above the body; in other groups they may be variously rolled, twisted or raised in repose.

Flight is not possible unless the temperature of the flight muscles is high enough, and therefore moths often vibrate their wings preparatory to flight. Diurnal species, such as butterflies, usually depend on the heat of the sun to raise their temperature sufficiently. A body temperature at least 10°C higher than that of the surrounding air is reached during flight in the hepialid *Trictena* (Tindale 1935), and up to 18°C higher in sphingids (Dorsett 1962).

Apart from normal dispersal movements, migratory flights of varying magnitude have long been observed in Lepidoptera (C. G. Johnson 1969). In Australia, the most conspicuous migrants are butterflies, especially the pierids *Anaphaeis java* and *Catopsilia* spp., the nymphalid *Vanessa kershawi*, and the hesperiid *Badamia exclamationis*. The noctuid moth, *Agrotis infusa*, is known to undertake a remarkable annual two-way migration (Common 1954b).

Variation due to either environmental or genetic factors is common in Lepidoptera. Seasonal variation, for example, is found in *A. infusa*: a sombre spring form with dark hind wings contrasts with a much paler autumn and winter form with whitish hind wings (Common 1958a). Distinct seasonal forms occur in many pierid butterflies such as *Eurema laeta* (Jones *et al.* 1985) and *Catopsilia pomona* (Rienks 1985). Many caterpillars are kentromorphic, a green or pale-coloured phase being characteristic of a low population level and a conspicuously striped (probably aposematic) or dark-coloured phase of a high population level. Geographical variation, which may be of either environmental or genetic origin, is well demonstrated in the butterflies, especially the Satyrinae. Two genetically distinct racial groups of *Tisiphone abeona* have been recognised in coastal south-eastern Australia, with an extremely variable population occupying a small zone of contact between them (G. Waterhouse 1928). Sexual dimorphism is marked in many Lepidoptera, with

the sexes of such extreme examples as *Epitymbia cosmota* having been described not only as separate species, but as distinct genera.

**Reproduction.** In diurnal butterflies and moths the males are attracted to females of the same species by visual stimuli, but in most nocturnal moths the males respond to sex pheromones disseminated by receptive females, sometimes over considerable distances. In a few species females are attracted to the pheromones disseminated by displaying males. Female sex pheromones are produced by dermal glands usually located intersegmentally between abdominal segments 8 and 9. Individual components of the pheromones or combinations of them play separate roles in the mating sequence. When the male has perceived the female, mating may be preceded by the emission of male pheromones which evoke the mating response in the female. These may be secreted by special glands of the abdomen, legs or wings, with androconia and extensile brushes of scales aiding in their dissemination.

Olfactory stimuli provided by the essential oils of the food plant are believed to induce oviposition. The average number of eggs laid varies from a few dozen to many thousands; more than 18 000 are laid by *Xyleutes* and *Abantiades*. The eggs may be deposited singly or in batches, near or on the food plant; the oviposition habits are characteristic of the species and often of the genus. Some of the Hepialidae scatter their eggs at random during flight, others in loose masses on the ground (some *Oncopera*); *Ptilomacra senex* (Cossidae) arranges its eggs in a cylindrical pattern around small twigs; *Epiphyas postvittana* and many other Tortricidae lay their scale-like eggs slightly overlapping one another in batches; many Limacodidae also lay scale-like eggs; *Persectania ewingii* and other hadenine Noctuidae insert their eggs with their wedge-shaped papillae anales beneath the leaf sheaths of grasses; and the Incurvarioidea and Eriocraniidae insert theirs into plant tissues with their sclerotised cutting ovipositors. In some species of *Monopis* (Tineidae) the fertilised eggs are retained in a grossly enlarged vagina until the embryo is mature; hatching follows immediately the eggs are laid.

Parthenogenesis, as a regular feature of the life cycle, has been reported only in special races of European Psychidae. Occasionally, however, it occurs in individuals of species which normally reproduce bisexually (e.g. Pieridae, *Galleria*).

**Immature Stages.** In some species the newly hatched larva makes its first meal of the chorion. Many leaf-miners tunnel direct from the egg into the leaf tissue beneath (e.g. Nepticulidae). Although most lepidopterous larvae are phytophagous, a few are carnivorous, feeding on the egg masses of other Lepidoptera (*Titanoceros*) or of spiders (*Stathmopoda*), on living ant larvae (some Lycaenidae, Cyclotornidae) or on scale insects (*Batrachedra*, *Stathmopoda*, *Catoblemma*). Cannibalism is not uncommon among phytophagous larvae reared in confined spaces (e.g. *Helicoverpa*, *Agrotis*, Lycaenidae), but probably does not occur commonly in nature unless populations are exceptionally dense. Some larvae feed on



materials of animal origin, such as wool and keratin (e.g. *Tineola*), digestion being permitted by the secretion of an enzyme which breaks the disulphide linkage of the wool molecule. A few species (Epipyropidae, early stages of Cyclotornidae) are ectoparasitic on leafhoppers.

There are few plant habitats that have not been exploited by Lepidoptera, and every part of the plant provides food: the roots, trunk, bark, branches, twigs, leaves, buds, flowers, fruits, seeds and galls, and fallen seeds, fruit or leaves. Larvae that feed in concealed situations, such as the borers, leaf- and bark-miners, leaf-tiers and case-bearers, usually belong to the more primitive families, whereas the exposed feeders, especially those that feed during the day, usually belong to the more advanced families.

Many people who live in inland Australia have observed that Lepidoptera at times are among the most abundant insects in dry country. Under such conditions, diurnal species, such as butterflies, are usually scarce. The most abundant are those whose larvae feed in concealment and so avoid desiccation. The adults are usually on the wing for only a few days, especially just after rain, during which time they mate and lay their eggs. Of special note are the Hepialidae and Cossidae, the larvae of which either tunnel in roots, or feed externally on roots which tap subterranean supplies of water. Some Gelechioidea which have effectively exploited the inland have larvae tunnelling in stems, galls or seed capsules, or living in concealed shelters. Certain other species of Lepidoptera utilise the rapidly responding vegetation which follows sporadic rains, emerging as adults, laying their eggs, and rapidly completing their larval development, before entering the soil and remaining quiescent as larvae or pupae until further rain falls. Included here are many herb-feeding species in the Noctuidae, Geometridae and Pyralidae.

Although concealment in itself provides some measure of protection from desiccation, rapid changes in temperature, and other physical hazards, it by no means protects the larva from potential parasites and predators. Even vertebrates, such as the yellow-tailed black cockatoo (McInnes and Carne 1978), are able to detect and extract wood-boring larvae and pupae from deep within tree trunks.

Larvae that feed in exposed situations have developed a remarkable range of adaptations which lessen potential hazards. Cryptic concealment, by means of green, grey and brown coloration, resembling that of the leaves, bark and other plant parts with which the insect associates, aids it to escape the attention of predators. The twig-like larvae of many Geometridae, and the larvae of Lasiocampidae merging with the branch to which they closely appress their hairs, are good examples. Once detected, the larva may then rely on an alternative mechanism to startle, or escape from, its enemy. Papilionid larvae display brightly coloured and pungent-smelling osmeteria; *Entometa* (Lasiocampidae) larvae arch their thorax and expose black, elliptical, mouth-shaped areas; many larvae rear up and strike at an intruder with the head, at the same time often regurgitating a brightly coloured fluid; and others feign death and drop to the

ground or lower themselves rapidly on a thread of silk. Similar mechanisms are exhibited by adult moths. When disturbed, many species suddenly display brightly coloured hind wings which were concealed beneath the procrystic fore wings while the insect was at rest. Adults of some Arctiidae and several other families feign death when handled, and *Rhodogastria* (Arctiidae) emits a pungent, yellow, frothy liquid from prothoracic glands. During flight Pyralidae and Noctuidae respond to the ultrasonic cries of bats by making vigorous evasive movements (Spangler 1988), and aposematically coloured Arctiidae respond by producing ultrasonic sounds which warn bats of their inedible properties (Fenton and Roeder 1974).

Aposematic or warning coloration, which might be associated with distasteful or injurious properties, is common in the diurnal larvae of several lepidopterous families. The brightly coloured bands found in *Danaus* and *Euploea* (Nymphalidae) and many Agaristinae (Noctuidae) probably discourage predators. Some of these species may be genuinely distasteful, whereas others benefit from the protection afforded by similar coloration. Day-flying moths frequently have aposematic colour patterns, some, such as the Ctenuchinae (Arctiidae) and Sesiidae, having orange and black bands on the abdomen and partially transparent wings resembling wasps. The orange and black body and transparent wings of the sphingid *Cephonodes kingii* suggest a large bumble bee, while the brown, yellow and black markings of the small stathmopodine *Snellenia lineata* (Plate 6, F), reinforced by its behaviour at flowers, bear a striking resemblance to the distasteful *Metriorrhynchus* beetles which also visit flowers. The larva of *Homodes* (Noctuidae) has a series of lateral, clubbed, thread-like processes which are constantly waved as it moves, giving it a startling resemblance to two of the *Oecophylla* ants which frequent the same host plant. Rothschild (1985) provided a review of aposematic Lepidoptera.

Hairy caterpillars generally seem to be distasteful to predators, although cuckoos and certain other birds are able to eat them with impunity. Modified setae of various kinds produce a stinging sensation if they contact the human skin, while others cause dermal rashes or urticaria. In *Doratifera* (Limaecodidae) paired, dorsal processes contain eversible tufts of brightly coloured stinging hairs, which resemble minute sea-anemones. Contact produces a sensation similar to a mild nettle sting. Hairy caterpillars of several families are able to cause skin rashes in humans (D. J. Lee 1975; Southcott 1978; J. O. Alexander 1984; Kawamoto and Kumada 1984). No Australian Lasiocampidae are known to do this, but in the Northern Hemisphere *Malacosoma* is notorious. Among the Bombycoidea, *Anthela nicotiae* (Anthelidae) and the gregarious *Panacela lewiniae* (Eupterotidae) can both cause skin rashes. Both in Australia and Europe the processionary caterpillars of the family Thaumetopoeidae are known to have urticating properties. The gregarious *Ochrogaster lunifer* is a good example. In Australia urticaria is most usually caused by larvae of the lymantriids *Euproctis edwardsii* and *Leptocneria reducta*. A few Australian



Arctiidae have urticating properties, including *Spilosoma glatignyi*. Further study is needed on the means by which larval setae cause urticaria, and the problem is complicated by the occurrence of human allergies.

**Natural Enemies.** At any stage in its life the lepidopteran may fall prey to a great variety of predators and parasites. Perhaps the greatest loss of eggs is due to parasitism by Chalcidoidea and Platygasteroidea. The larvae provide food for mites, spiders, wasps (especially Vespidae) and a great number of vertebrates, especially birds. The fat-rich larvae of certain Cossidae were important items in the diet of the Aborigines. Both larvae and pupae are prone to parasitism by Mermithidae (Nematoda), Chalcidoidea, Braconidae, Ichneumonidae and Tachinidae. Bacterial and viral diseases at times take their toll of larvae and pupae, drastically reducing populations. Adult moths and butterflies are preyed upon mainly by vertebrates, birds probably destroying the greatest numbers. Many moths, especially those which shelter in the leaf litter, have parasitic mites attached to their antennae and other parts of their bodies, while some Noctuidae (e.g. *Mythimna convecta*) harbour colonies of mites within their tympanal organs (Treat 1975). Bogong moths are parasitised in their aestivation camps by the mermithid worms *Amphimermis bogongae* and *Hexameris cavicola*, and were also used as food by the Aborigines.

**Economic Significance.** Being predominantly phytophagous, the Lepidoptera contribute substantially to the economic losses suffered by agricultural crop plants. In Australia the majority of lepidopterous pests are native species, some of which occur naturally also in New Guinea and South-East Asia. Of special note are the underground grass grubs (Hepialidae), borers (Hepialidae, Cossidae, Sesiidae, Xyloryctinae), leaf-miners (Incurvariidae, Gracillariidae), leaf-rollers (Tortricidae), leaf-tiers and web-worms (Pyrallidae), forest defoliators (Limacodidae, Geometridae, Eupterotidae, Nolidae), and cutworms and armyworms (Noctuidae). The introduced species are mainly cosmopolitan pests of stored food-stuffs and fibres (Tineidae, Oecophoridae, Gelechiidae, Pyralidae), and of orchard (Tortricidae) and vegetable crops (Plutellidae, Gelechiidae, Pieridae).

Several Lepidoptera are obviously beneficial to humans. Species which prey on coccids (*Batrachedra*, *Stathmopoda*, *Catoblema*) and parasitic species (Epi-pyropidae) which attack leafhoppers presumably assist in the control of these pests. *Titanoceros* destroys the egg

masses of the bag-shelter moth (*Ochrogaster*), a minor pest of shade and fodder trees. Other species, such as those that assist in reducing leaf litter to humus, must be beneficial in a less tangible way. A few exotic Lepidoptera have been introduced to assist in the control of major introduced weeds. Of these the most outstanding has been the South American pyralid *Cactoblastis* which effectively controlled prickly pear (*Opuntia* spp.) in Qld and N.S.W. (p. 232).

### Special Features of the Australian Fauna

The major families of Lepidoptera are all represented in Australia, but the relative abundance of several groups differs markedly from that of other continents. Some sections apparently represent a Gondwanan fauna, while others are of Oriental origin, upon which has probably been superimposed further Oriental and Papuan elements in several waves.

Archaic families, such as the Hepialidae, Heliozelidae, Incurvariidae, Palaephatidae, Cossidae and Castniidae, are relatively richly represented, but whether this radiation took place in the absence of more advanced groups in the continent, or in competition with those groups in response to increasing aridity, is not clear. The larvae of these families are either leaf-miners or are adapted to feed within stems and roots or deep in the soil externally on roots; such behaviour patterns would greatly favour their survival in an arid environment. Concealed feeding and an outstanding adaptation to a dominant flora of *Eucalyptus* and *Acacia* have probably also contributed to the abundance of species in the Oecophoridae which comprise more than a quarter of the fauna; oecophorids are especially abundant in the *Eucalyptus* forests and woodlands in both coastal and inland areas.

Groups which probably have reached Australia more recently, and which are still most abundant in the north, include the Sesiidae, Lecithoceridae, Papilionidae, Pieridae, Uraniidae, Sphingidae, Lymantriidae and Aganaiidae, together with large sections of the Gelechiidae, Pyralidae, Geometridae, Notodontidae, Arctiidae and Noctuidae. Nevertheless, some of these families contain large blocks of endemic genera, notably the Oenochrominae (Geometridae). The Lophocoronidae, Anomosetidae, Cyclotornidae and Carthaeidae are confined to Australia, and Hypertrophidae and Anthelidae to Australia and New Guinea.

### CLASSIFICATION

Order LEPIDOPTERA  
(20816 Australian spp.)

Suborder ZEUGLOPTERA (9)

MICROPTERIGOIDEA (9)

1. Micropterigidae (9)

Suborder AGLOSSATA (1)

AGATHIPHAGOIDEA (1)

2. Agathiphagidae (1)

Suborder HETEROBATHMIINA (0)

HETEROBATHMIOIDEA (0)

Heterobathmiidae (0)

- Infraorder *Dacnonypha s.l.* (0)  
 ERIOCRANIOIDEA *s.l.* (0)  
     Eriocraniidae (0)  
     Acanthopteroctetidae (0)  
     Catapterigidae (0)  
 Infraorder *Neopseustina* (0)  
 NEOPSEUSTOIDEA (0)  
     Neopseustidae (0)  
 Infraorder *Lophocoronina* (6)  
 LOPHOCORONOIDEA (6)  
     3. Lophocoronidae (6)
- TINEOIDEA (1325)  
     13. Psychidae (353)  
         Arrhenophanidae (0)  
         Pseudarbelidae (0)  
     14. Eriocottidae (1)  
     15. Tineidae (440)  
     16. Roeslerstammiidae (42)  
     17. Galacticidae (10)  
     18. Bucculatricidae (28)  
     19. Douglasiidae (1)  
     20. Gracillariidae (450)  
 YPONOMEUTOIDEA (543)  
     21. Yponomeutidae (60)  
     22. Argysthiidae (1)  
         Ypsolophidae (0)  
     23. Plutellidae (78)  
     24. Glyphipterigidae (240)  
     25. Heliodinidae (4)  
     26. Lyonetiidae (160)  
 GELECHIOIDEA (8690)  
     27. Oecophoridae (5550)  
     28. Batrachedridae (50)  
     29. Hypertrophidae (200)  
     30. Depressariidae (120)  
     31. Coleophoridae (30)  
     32. Elachistidae (30)  
         Blastodacnidae (0)  
     33. Agonoxenidae (1)  
     34. Ethmiidae (14)  
     35. Blastobasidae (25)  
         Morphidae (0)  
     36. Cosmopterigidae (850)  
     37. Gelechiidae (1580)  
         Symmocidae (0)  
         Holcopogonidae (0)  
     38. Lecithoceridae (205)  
     39. Scythrididae (35)  
 COSSOIDEA (205)  
     40. Cossidae (202)  
         Metarbelidae (0)  
     41. Dudgeoneidae (3)  
 TORTRICOIDEA (1230)  
     42. Tortricidae (1230)  
 CASTNIOIDEA (45)  
     43. Castniidae (45)
- Suborder GLOSSATA (0)  
 Infraorder *Exoporia* (154)  
 MNESARCHAEOIDEA (0)  
     Mnesarchaeidae (0)  
 HEPIALOIDEA (154)  
     4. Palaeosetidae (2)  
         Neotheoridae (0)  
     5. Anomosetidae (1)  
         Prototheoridae (0)  
     6. Hepialidae *s.l.* (151)  
 Infraorder *Heteroneura* (20646)  
 NEPTICULOIDEA (330)  
     7. Nepticulidae (250)  
     8. Opostegidae (80)
- Series DITRYZIA (20103)  
 SESIOIDEA (90)  
     44. Brachodidae (45)  
     45. Sesiidae (19)  
     46. Choreutidae (26)  
 ZYGAENOIDEA (227)  
     Heterogynidae (0)  
     Megalopygidae (0)  
     Chrysopolomidae (0)  
     Somabrachyidae (0)  
     Dalceridae (0)  
     47. Zygaenidae (56)  
     48. Limacodidae (115)  
     49. Epipyropidae (16)  
     50. Cyclotornidae (40)  
 IMMOIDEA (20)  
     51. Immidae (20)  
 COPROMORPHOIDEA (126)  
     52. Copromorphidae (18)  
     53. Carposinidae (108)  
 SCHRECKENSTEINIOIDEA (0)  
     Schreckensteiniidae (0)  
 URODOIDEA (0)  
     Urodidae (0)  
 EPERMENIOIDEA (30)  
     54. Epermeniidae (30)  
 ALUCITOIDEA (34)  
     55. Tineodidae (14)  
     56. Alucitidae (20)  
 PTEROPHOROIDEA (40)  
     57. Pterophoridae (40)  
 HYBLAEOIDEA (5)  
     58. Hyblaeidae (5)  
 THYRIDOIDEA (81)  
     59. Thyrididae (81)  
 PYRALOIDEA (1670)  
     Lathrotelidae (0)  
     60. Pyralidae (1670)  
 GEOMETROIDEA (2310)  
     61. Geometridae (2310)  
 AXIOIDEA (0)  
     Axiidae (0)  
 DREPANOIDEA (13)  
     62. Drepanidae (13)  
 URANIOIDEA (36)  
     63. Uraniidae (36)
- INCURVARIOIDEA (183)  
     9. Heliozelidae (45)  
     10. Adelidae (28)  
         Crimpterygidae (0)  
     11. Incurvariidae (110)  
         Cecidosidae (0)  
         Prodoxidae (0)  
 PALAEPHATOIDEA (30)  
     12. Palaephatidae (30)  
 TISCHERIOIDEA (0)  
     Tischeriidae (0)
- Unassoc. with superfamily (0)  
     Sematuridae  
     (Apoprogonidae) (0)  
     Epicopeiidae (0)  
 CALLIDULOIDEA (0)  
     Callidulidae (0)  
     Pterothysanidae (0)  
 HESPERIOIDEA (122)  
     64. Hesperidae (122)  
 HEDYLOIDEA  
     Hedylidae (0)  
 PAPILIONOIDEA (275)  
     65. Papilionidae (18)  
     66. Pieridae (32)  
     67. Nymphalidae (85)  
     68. Lycaenidae (140)  
 MIMALLONOIDEA (0)  
     Mimallonidae (0)  
 BOMBYCOIDEA (245)  
     Endromidae (0)  
     69. Lasiocampidae (90)  
     70. Anthelidae (121)  
     Apatelodidae (0)  
     71. Eupterotidae (14)  
         Hibrildidae (0)  
         Lemoniidae (0)  
     72. Bombycidae (3)  
         Brahmaeidae (0)  
     73. Carthaeidae (1)  
         Oxytenidae (0)  
         Cercophanidae (0)  
     74. Saturniidae (16)  
         Ratardidae (0)  
 SPHINGOIDEA (65)  
     75. Sphingidae (65)  
 NOCTUOIDEA (2676)  
     76. Notodontidae (145)  
     77. Thaumetopoeidae (55)  
         Dioptidae (0)  
         Thyretidae (0)  
     78. Lymantriidae (129)  
     79. Arctiidae (342)  
     80. Aganidae (8)  
     81. Hermiidae (40)  
     82. Noctuidae (1957)



The Lepidoptera are here divided into four suborders, Zeugloptera, Aglossata, Heterobathmiina and Glossata (Kristensen and Nielsen 1983; Kristensen 1984e). The Glossata, the proboscis-bearing Lepidoptera, are further subdivided into several infraorders of which the Ditrysia of the infraorder Heteroneura contain about 98% of all species. A tentative phylogeny including all non-Ditryisian families is shown in Fig. 41.13A. While the monophyly of many groups is now firmly established, major problems, such as the sister-group of the Ditrysia

and the possible monophyly of the so-called Monotrysia (Nepticuloidea, Incurvarioidea, Palaephatoidea and Tischerioidea), remain without a satisfactory solution. Recent reviews of the phylogeny of the so-called 'primitive' non-Ditryisian Lepidoptera were given by Kristensen (1984e), Nielsen (1985a,b, 1989) and D. R. Davis (1986). Minet (1986) and Nielsen (1989) provided the most recent account of the Ditrysia; a phylogeny for the ditryisian superfamilies is shown in Fig. 41.13B.

The classification prepared for this chapter is also used



Fig. 41.13 Tentative cladograms summarising the phylogeny of the Lepidoptera: A, phylogeny of primitive (non-ditryisian) families; B, phylogeny of ditryisian superfamilies (Sphingoidea are included with Bombycoidea). After Nielsen (1989). [S. Smith]

by Common (1990) and Nielsen *et al.* (in press). The latter explains changes introduced here.

A more detailed account of the Australian moth fauna is provided by Common (1990). Munroe (1982) provided the most recent synopsis of all families. J. D. Holloway *et al.* (1987) give keys to families and a general account of all families with emphasis on groups of economic importance, and Scoble (in press) offers a review of the biology and classification of the entire order. Inoue *et al.* (1982) illustrate structural details and adult moths of all families occurring in Japan, and Dugdale (1988b) offers an annotated catalogue of the entire New Zealand fauna. Little

work has been published on the larvae of Australian Lepidoptera, but the detailed information in Stehr (1987b) and the practical keys in Carter (1987) are useful. The above titles cover almost all families and are rarely referred to in the text below.

Hollis (1980) provided a useful guide to important references with these organised systematically and subdivided geographically. Moulds (1977) dealt with the literature on Australian butterflies, and the literature lists in Common (1990) and Nielsen *et al.* (in press) contain the most important publications relevant to the Australian fauna.

## KEY TO THE SUBORDERS OF LEPIDOPTERA

1. Maxillary galeae forming a proboscis (Fig. 41.18D), usually spirally coiled in repose, sometimes secondarily reduced or absent; mandibles small and non-functional. Larvae with articulated spinneret (Figs 41.10A, B) ..... GLOSSATA (p. 837)
- Maxillary galeae unmodified, not forming a proboscis (Figs 41.15C, F); mandibles (Figs 41.15B, E) functional. Larvae without a spinneret ..... 2
- 2(1). Labial palps long; fore tibia with a single apical spur, mid tibia with 2 pairs of spurs. Larvae without cranial ecdysial line; with one-segmented antennae and labial palps ..... AGLOSSATA (p. 835)
- Labial palps short; fore and mid tibial spurs absent. Larvae with ecdysial line; with more than one segment in antennae and labial palps ..... 3
- 3(2). Antennal flagellum with 'ascoids' (see below); tentorium 'normal', H-shaped; fore wing with  $R_1$  forked. Larvae without adfrontal ridge, with 5 or 6 stemmata ..... ZEUGLOPTERA (p. 834)
- Antennal flagellum without 'ascoids'; anterior tentorial arms fused, tentorium Y-shaped; fore wing with  $R_1$  simple. Larvae with adfrontal ridge and 7 stemmata ..... Heterobathmiina

## Suborder ZEUGLOPTERA

The suborder Zeugloptera contains only the one family, Micropterigidae, distributed world-wide. Kristensen (1984c) summarises autapomorphies.

## Superfamily MICROPTERIGOIDEA

1. *Micropterigidae* (Fig. 41.17A). Small; head (Fig. 41.15A) with raised hair-scales; ocelli present; chaetosemata absent; antennae moniliform, submoniliform or filiiform, flagellar segments with multibranching sensilla ('ascoids'); labrum centrally unsclerotised; epipharynx with asymmetrical armature; maxillary palps 5-segmented (Fig. 41.15c); labial palps short, 2- or 3-segmented; fore tibial epiphysis present or absent; tibial spurs 0-0-4; fore wing (Fig. 41.14A) with small jugum, humeral vein vestigial,  $Sc$  forked,  $Sc_2$ - $R_1$  cross-vein sometimes present, chorda present,  $R_1$  sometimes forked, cross-veins  $CuA$ - $CuP$  and  $CuP$ - $2A$  often present; hind wing as fore wing or with  $Sc_2$  fused with  $R_1$ ,  $Sc$  and  $R_1$  confluent in 'Australian group' taxa,  $A$  often simple; abdomen with or without  $S5$  gland; male  $S8$  more or less unsclerotised; ovipositor lobes retractile, non-piercing, segments 8 and 9 without apophyses. Eggs with specialised chorion structure (Chauvin and Chauvin 1980). Larva slug-like, prognathous, with 6 or 5 stemmata; antenna 3-segmented; without adfrontal ridges and ecdysial lines; salivary orifice not on spinneret; body hexagonal in cross-section; chaetotaxy reduced, with hair-like to claviform setae; thoracic legs 3- or 4-segmented, with apical claw; non-muscular prolegs devoid of crochets often on first 8 abdominal segments; some species with plastron. Pupa

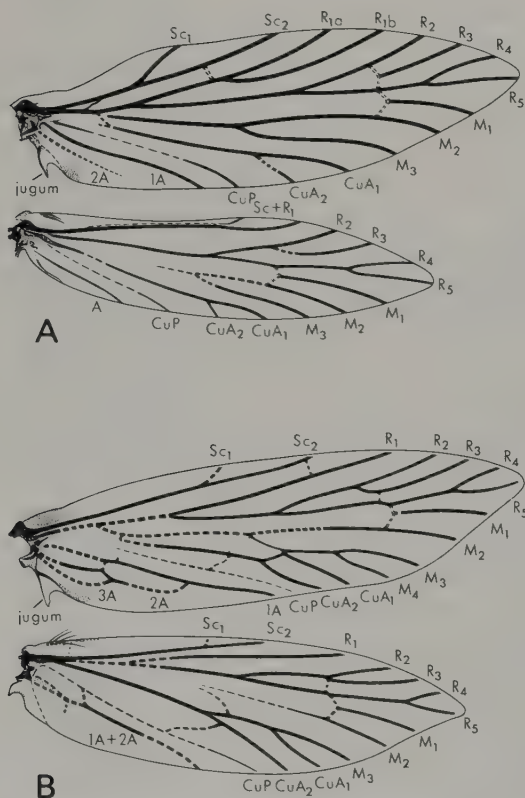


Fig. 41.14 Wing venation of Zeugloptera and Aglossata: A, *Sabatinca*, Micropterigidae; B, *Agathiphaea*, Agathiphaeidae.

[J. Wedgbrow]



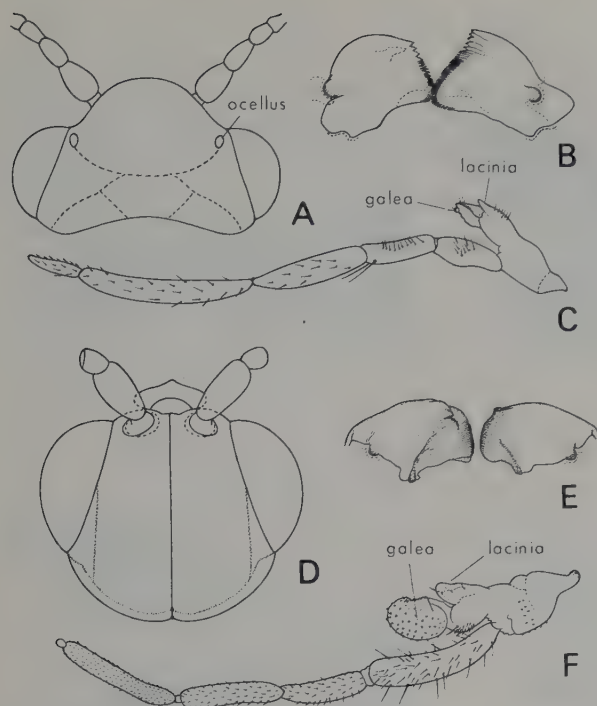


Fig. 41.15 A–C, head, mandibles and maxilla of *Sabatinca*, Micropterigidae; D–F, head, mandibles and maxilla of *Agathiphaga*, Agathiphagidae. [B. Rankin]

with pointed mandibles, used for opening the cocoon, and free appendages.

The nine Australian species of Micropterigidae all occur in rainforest in eastern Australia and Tas. They are currently placed in *Sabatinca s.l.*, but were divided into two groups by Gibbs (1983). *S. porphyrodes* is restricted to the Ravenshoe area in northern Qld; the remaining species belong to the 'Australian group' and include *S. sterops*, a tiny golden species from northern Qld, and several, such as *S. calliplaca* (Fig. 41.17A), which are very similar, deep purplish and with whitish transverse bands across the fore wings. Adults are diurnal and fly in filtered sunshine in damp forest localities; females (and sometimes males) come to light. Adults feed on pollen and spores and may aggregate at food sources. In New Zealand the larvae of *Sabatinca* feed on liverworts and one type believed to represent the 'Australian group' has been taken from within rotten logs in Qld; other exotic species feed on the lower leaves of grasses and other herbaceous plants. They pupate in a tough, silken, oval cocoon in the soil or detritus. The moths fly during early spring and early summer (Aug.–Sept. in Qld). [Carter and Dugdale 1982; Kristensen 1984c; Kristensen and Nielsen 1979, 1982]

### Suborder AGLOSSATA

This suborder contains only the family Agathiphagidae. Autapomorphies are listed by Kristensen (1984e).

### Superfamily AGATHIPHAGOIDEA

**2. Agathiphagidae** (kauri moths) (Fig. 41.17B). Small; head (Fig. 41.15D) elongate and flattened, with hair-scales; anterior tentorial arms Y-shaped; ocelli and

chaetosemata absent; antennae filiform, with numerous sensilla coeloconica on base of each flagellar segment and scales in 2 annuli per segment; infrabuccal pouch without a 'trituration basket'; mandibles large, with powerful musculature and devoid of cusps; maxilla (Fig. 41.15F) with lacinia present; galea a prominent elongate lobe with concave inner surface; maxillary palps 5-segmented, folded; labial palps 3-segmented; fore tibial epiphysis present; tibial spurs 1-4-4; fore wing (Fig. 41.14B) with prominent jugum, Sc forked but Sc<sub>1</sub> weak, R<sub>2</sub> and R<sub>3</sub> forked, R<sub>4</sub> and R<sub>5</sub> forked, sometimes with cross-veins Sc<sub>2</sub>-R<sub>1</sub> and R<sub>3</sub>-R<sub>4+5</sub>, R<sub>5</sub> to apex or termen, M stem present or vestigial in cell, 3 or 4 M veins present, CuP weak with cross-veins M-CuP and CuP-A, A veins confluent distally; hind wing as fore wing but A fork short; cuticle weakly melanised; male only with paired S5 gland processes, gland a long, twisted tube; male with long, slender valvae; female with extensible, non-piercing ovipositor, both T8 and S8 with apophyses, posterior apophyses fused posteriorly. Larva hypognathous, apodous, stout, without adfrontal ridges and distinct ecdysial lines, with 2 pairs of vestigial stemmata, 1-segmented antennae, and salivary orifice not on spinneret (Kristensen 1984b). Pupa with huge asymmetrical mandibles and free appendages; in an oval cell within seed of *Agathis*.

The family comprises only a single genus, *Agathiphaga*, with two species, *A. queenslandensis* (Fig. 41.17B), in eastern Qld, and *A. vitiensis* in the south-west Pacific. Very few adults of *Agathiphaga* have been collected; the moths are nocturnal, come to light and superficially resemble caddis-flies. Little is known about the life history: the eggs are thought to be laid beneath the scales of *Agathis* cones; the larva excavates practically all of the inside of the seed; when feeding is completed it lines its cell with a very resistant, inner layer and an outer layer of compressed frass; pupation sometimes is delayed for four

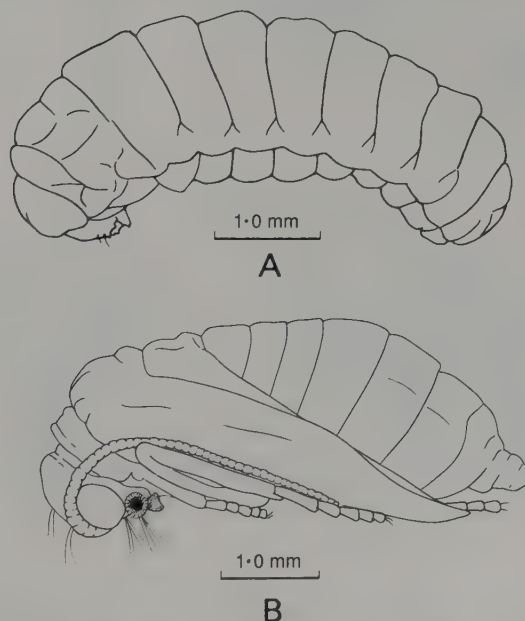


Fig. 41.16 *Agathiphaga*, Agathiphagidae: A, larva; B, pupa

[I. F. B. Common]

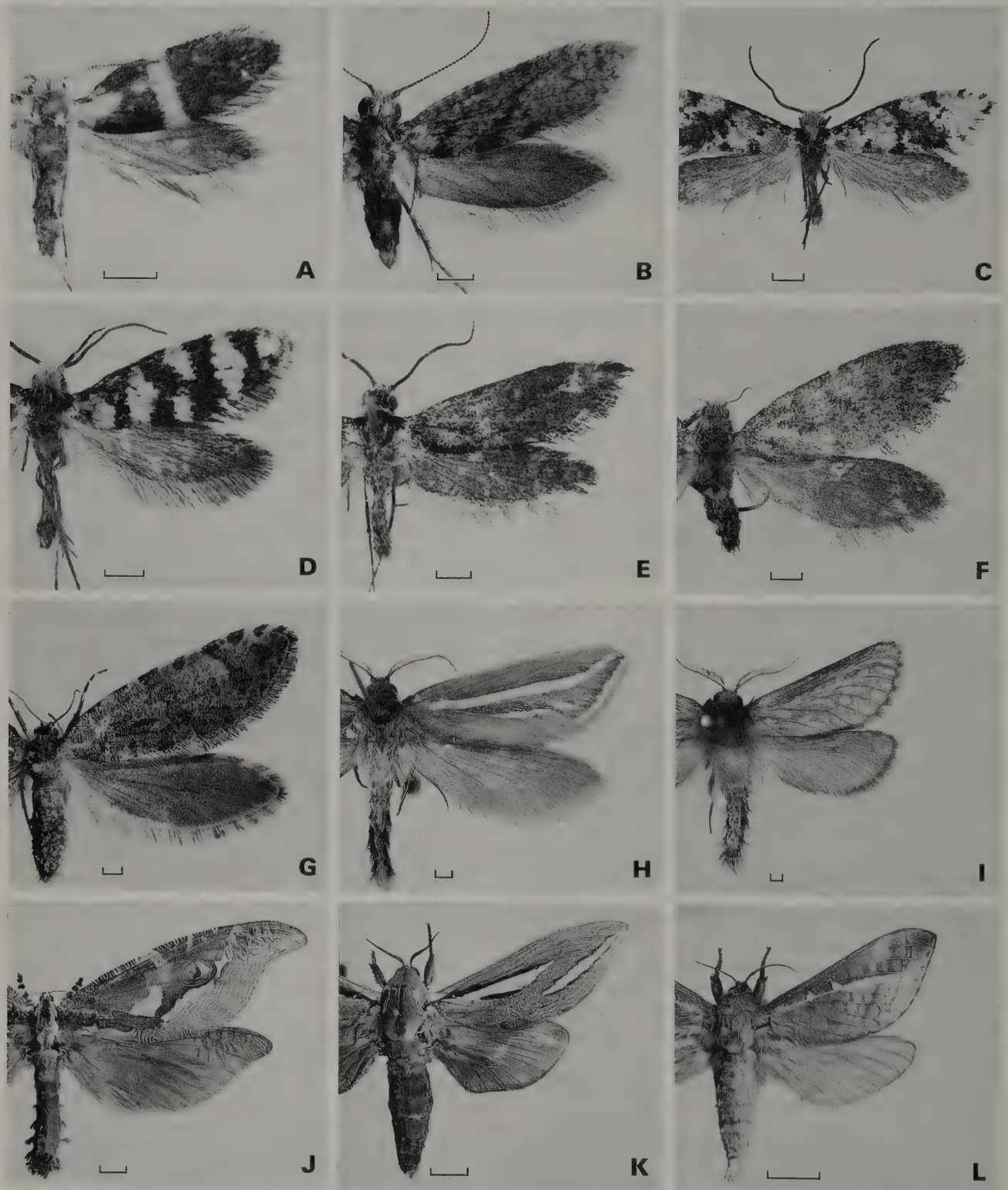


Fig. 41.17 A, *Sabatinca calliplaca*, Micropterigidae; B, *Agathiphaga queenslandensis*, Agathiphagidae; C, *Lophocorona astiptica*, D, *Lophocorona* sp. A, E, *Lophocorona* sp. B, Lophocoronidae; F, *Palaeoses scholastica*, Palaeosetidae; G, *Anomoses hylecoetes*, Anomosetidae; H, *Fraus orientalis*, I, *Fraus polyspila*, J, *Zelotypia stacyi*, K, *Abantiades magnificus*, L, *Oxycanus diremptus*, Hepialidae. Scales: A-I = 1 mm; J-L = 10 mm. [J. Green, C. Lourandos]



years. The pupa has extremely large mandibles with which the pharate adult grinds a circular exit hole in the cell prior to ecdysis. Although the larvae sometimes occur commonly, few adults have been reared. [Common 1973; Robinson and Tuck 1976; Kristensen and Nielsen 1983; Kristensen 1984b, d]

### Suborder GLOSSATA

This suborder (Fig. 41.13A) contains the bulk of the Lepidoptera. Autapomorphies listed by Kristensen (1984e) include the presence of a proboscis, the absence of functional mandibles in the post-pharate adult and the presence of an articulated spinneret in the larva.

#### *Key to Ditrysia and the Non-Ditrysiian Glossata Known in Australia*

1. Fore wing with a projecting jugum ..... 2  
Fore wing with a retinaculum, hind wing with a frenulum ..... 3
- 2(1). Fore wing with both  $R_4$  and  $R_5$  to termen well removed from apex (Fig. 41.20) ..... HEPIALOIDEA (p. 838)  
Fore wing with  $R_4$  to costa before apex and  $R_5$  to termen (Fig. 41.19) ..... LOPHOCORONOIDEA (p. 837)
- 3(1). Pseudofrenular bristles absent; S2 with apodemes and without postspiracular connection to T1; ♀ genitalia ditrysiian ..... DITRYSIA (p. 844)  
Pseudofrenular bristles usually present (Fig. 41.24); S2 without apodemes and usually with postspiracular connection to T1; ♀ genitalia monotrysiian ..... 4
- 4(3). Antennal scape with eye-cap (Fig. 41.22A); hind tibiae with prominent spines ..... NEPTICULOIDEA (p. 841)  
Antennal scape without eye-cap; hind tibiae without spines ..... 5
- 5(4). Proboscis scaled; ♂ valvae with prominent, blunt spines often forming comb (pectinifer); ovipositor piercing, without medial sensory ridge ..... INCURVARIOIDEA (p. 842)  
Proboscis unscaled; ♂ valvae without prominent, blunt spines; ovipositor non-piercing, with medial sensory ridge ..... PALAEPHATOIDEA (p. 844)

#### Clade MYOGLOSSATA:

infraorders LOPHOCORONINA, NEOPSEUSTINA,  
EXOPORIA and HETERONEURA

While the proboscis of the Eriocraniidae is devoid of intrinsic musculature, the proboscis of the Myoglossata contains either simple, longitudinal (non-ditrysiian Myoglossata) or highly complex (Ditrysia) musculature (Kristensen and Nielsen 1981b). The family Lophocoronidae is devoid of proboscis musculature and hence can be included in the Myoglossata only if it is assumed that this musculature is lost secondarily; the evidence bearing on this issue is ambiguous (Nielsen and Kristensen unpubl.). Presence of normal-type scales is an Acanthopteroctetidae and myoglossatan autapomorphy.

#### Superfamily LOPHOCORONOIDEA

**3. Lophocoronidae** (Figs 41.17C–E). Very small; head (Figs 41.18A, B) with long, raised, slender hair-scales; ocelli and chaetosemata absent; antennae filiform, to middle of fore wing, with slender scales scattered over entire surface of flagellar segments, articulation of antenna base dicondylous; labrum without pilifers; mandibles simple lobes, devoid of muscles; proboscis (Fig. 41.18D) short and delicate, 0.6 times head capsule height, without intrinsic musculature; maxillary palps 5-segmented, flexed at joints 1/2 and 3/4; labial palps 3-segmented, 0.6 times length of maxillary palps; fore tibial epiphysis absent, tibial spurs 0-2-4; fore wing with small jugum, with only one type of scale; fore wing (Fig. 41.19) with Sc forked, with or without cross-vein Sc-Rs,  $R_2$  and  $R_3$  stalked,  $R_4$  and  $R_5$  stalked,  $R_5$  to termen, inter Rs cross-vein present or absent, M-stem present in cell, CuP present, A veins vestigial at base, with or without CuP-A cross-vein; hind wing with Sc and  $R_1$  simple and CuP present; abdomen with paired S5 gland processes; male genitalia with paired, rounded dorsal lobes with promi-

nent sensilla, valvae bilobed; female with piercing ovipositor (Fig. 41.18E). Immature stages unknown.

The Lophocoronidae are a small family endemic to Australia, with only six species in the genus *Lophocorona*. They occur in southern Australia in low-rainfall areas from west of Coolgardie (W.A.) along the Great Australian Bight to the Eyre Peninsula (S.A.) in mallee and dry sclerophyll forest, at Canberra (A.C.T.) and north-west of Wollongong (N.S.W.) in dry sclerophyll forest. Five species are white with distinct, fuscous, transverse bands or with a dark suffusion in the middle of the wing (Figs 41.17C, D); one species has uniform blackish brown fore wings (Fig. 41.17E) and flies in mid summer while all other species fly during April and May. Males come to light early in the evening; a female taken at light came late in the evening. The immature stages are unknown but the piercing ovipositor suggests that the larvae are internal borers or leaf-miners and the absence of mandibular muscles in the adult moth shows that the pupa must be adecticous. [Common 1973]

#### Clade NEOLEPIDOPTERA:

infraorders EXOPORIA and HETERONEURA

This clade consists of the Exoporia and the Heteroneura (Fig. 41.13A); the monophyly of the Neolepidoptera is supported by an impressive list of autapomorphies (Kristensen 1984e) including the adecticous, obtect pupa with dorsal abdominal spines and the larva with musculate, crochet-bearing abdominal prolegs (reduced in many leaf-mining groups).

#### Infraorder EXOPORIA

The infraorder (Fig. 41.13A) comprises the superfamilies Mnesarchaeoidea, which is endemic to New Zealand, and Hepialoidea. Autapomorphies include a dicondylous articulation of the antennal base, wing scales with sec-

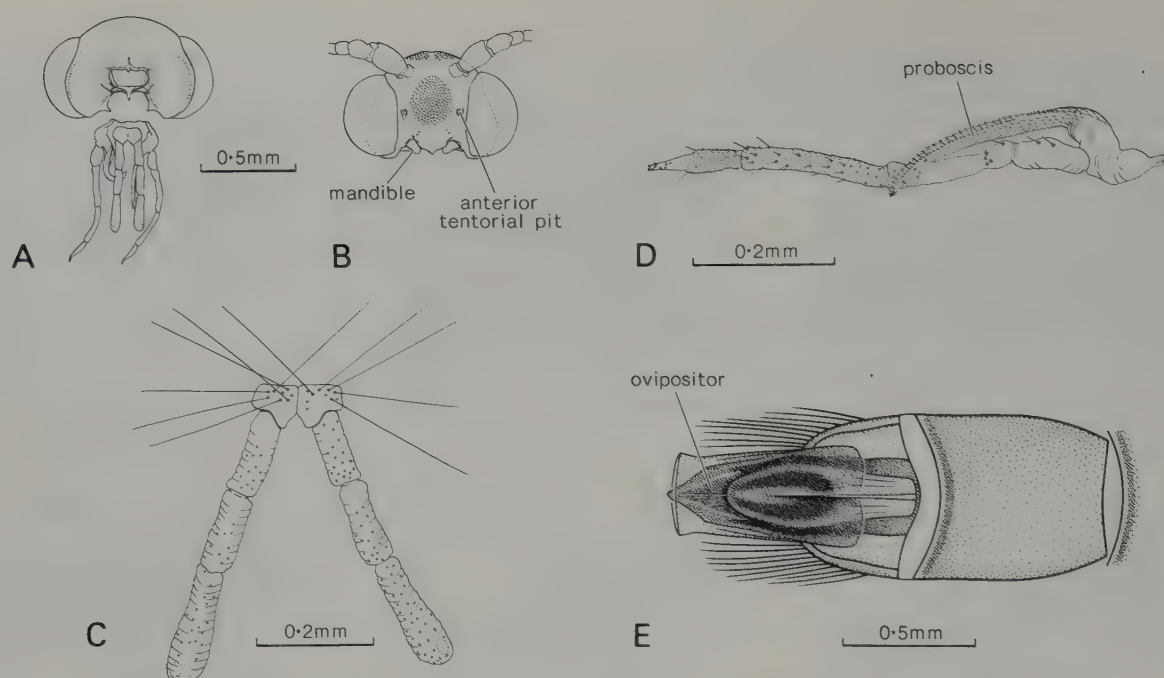


Fig. 41.18 Lophocoronidae: A, B, head and mouth-parts, posterior and anterior; C, labial palps; D, maxilla; E, female postabdomen, dorsal, of *Lophocorona*. [A–D by I. F. B. Common; E by S. P. Kim]

ondary ridges, male genitalia without prominently sclerotised intromittent organ and female genitalia exoporian (Kristensen 1984e). As in other Neolepidoptera (*Exoporia* + *Heteroneura*) the pupae are adecticous, obtect and have rows of spines on several abdominal segments and the larvae have crochet-bearing prolegs.

#### Superfamily HEPIALOIDEA

Small to very large; antennae short, with dense mat of

cuticular projections; ocelli and chaetosemata absent; mandibles small, non-functional; proboscis small or absent; maxillary palps minute or absent; labial palps 3-, 2- or 1-segmented; prelabium often prominent; wings usually with microtrichia; fore wing with humeral vein, Sc simple or forked;  $R_4$  to termen well below apex; CuP present, at least in basal half, A veins fused except at extreme base; hind wing as fore wing, Sc usually simple, CuP present, at least distally.

#### Key to the Families of Hepialoidea Known in Australia

1. Spurs 0-2-4 ..... **Anomosetidae** (p. 838)
- Spurs 0-0-0 (Australian species) ..... 2
- 2(1). Fore wing with inter-M cross-vein; ♂ without lateral protuberance on abdominal segment 6 ..... **Hepialidae s.l.** (p. 840)
- Fore wing without inter-M cross-vein; ♂ with lateral protuberance on abdominal segment 6 (Australian species) ..... **Palaeosetidae** (p. 838)

**4. Palaeosetidae** (Fig. 41.17F). Small; head with broad lamellar scales and scattered hair-scales; antennae covered with lamellar scales on proximal third, devoid of scales on distal two-thirds; mandibles and maxillae absent; labial palps short, 2-segmented; epiphysis absent; spurs absent; hind tibia not modified; wings aculeate; jugum small; fore wing (Fig. 41.20A) with Sc forked, inter-M and M-CuA cross-veins absent, with one A vein; male with prominent protuberance with specialised scales on each side of abdominal segment 6.

In the strict sense, as described above, the family probably contains only the endemic Australian genus *Palaeoses* (Turner 1922) with one named species, *P.*

*scholastica* (Fig. 41.17F), from southern Qld and one unnamed species from northern Qld. *Ogygioses* from Taiwan, *Genustes* from Assam and *Osrhoes* from Columbia are included in Palaeosetidae s.l. but the monophyly of this assemblage is questionable (Kristensen 1978a; Nielsen and Scoble 1986). *P. scholastica*, a small, dark brown species less than 18 mm in wingspan, is taken by sweeping foliage in rainforest.

**5. Anomosetidae** (Fig. 41.17G). Small; head with lamellar scales and scattered long hair-scales; flagellar segments with long, pointed, brown hair-scales; proboscis a short vestige; maxillary palps minute; labial palps 3-segmented, longer than head capsule; epiphysis absent;



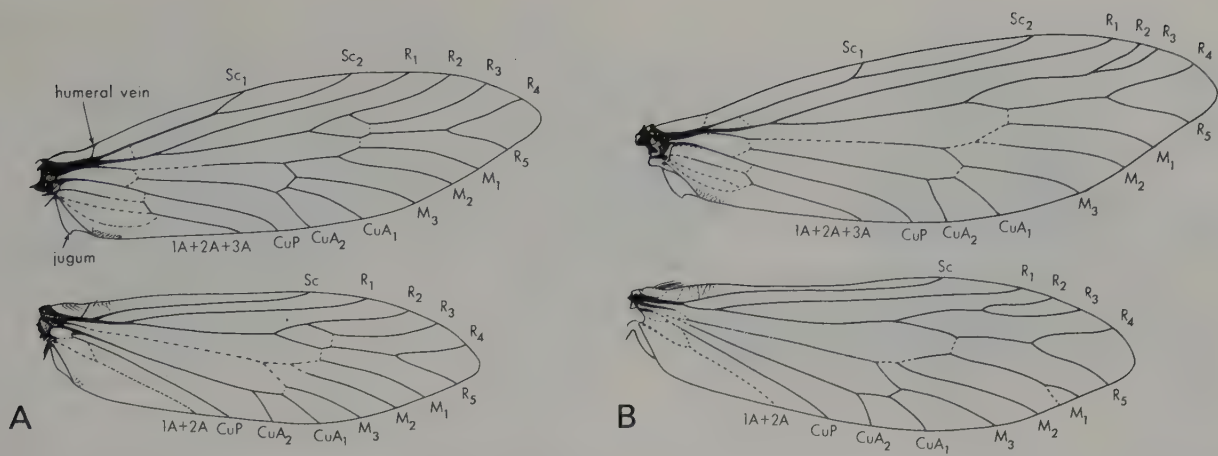


Fig. 41.19 Wing venation of Lophocoronidae: A, *Lophocorona pediasia*; B, *L. melanora*.

[I. F. B. Common]

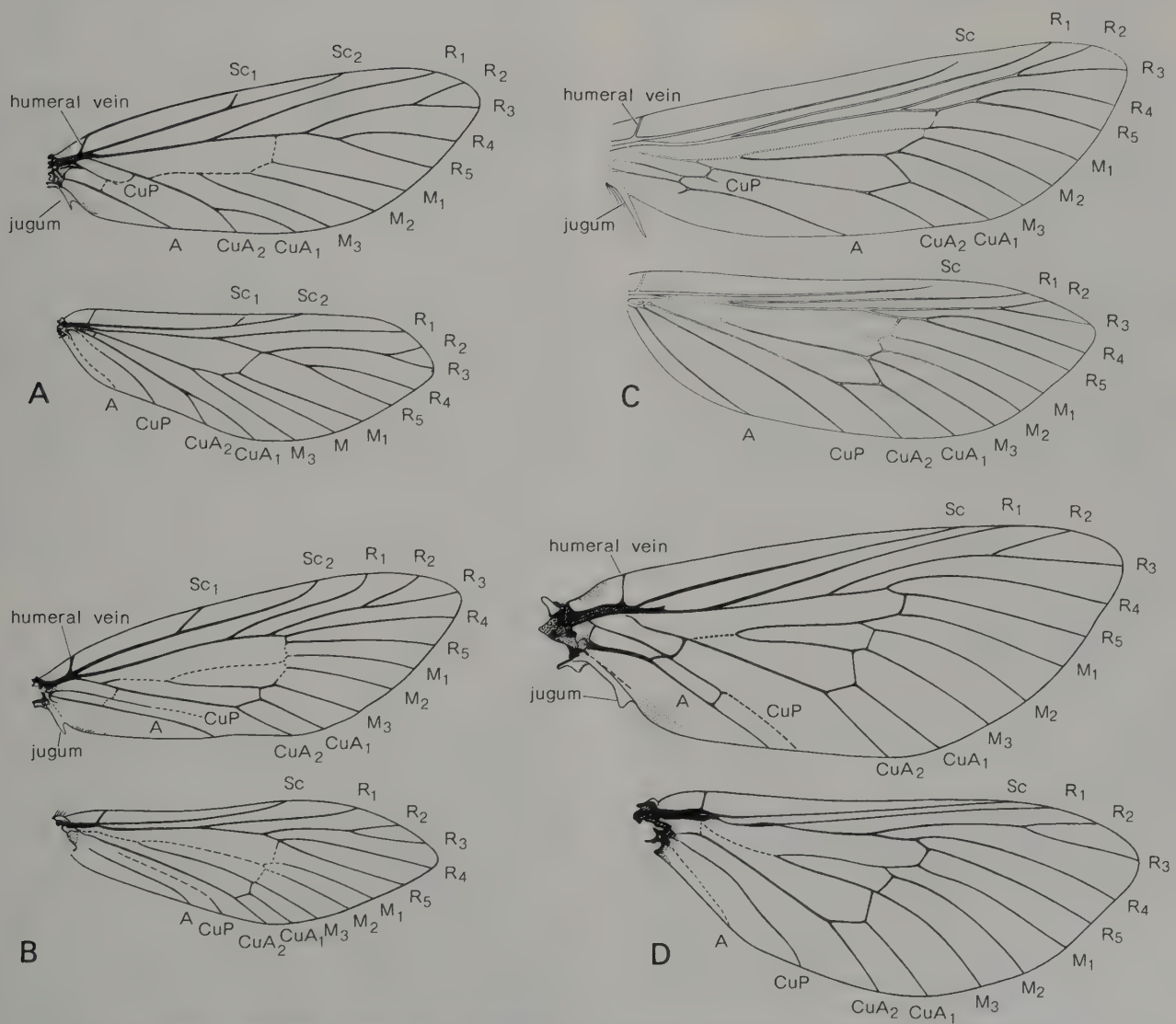


Fig. 41.20 Wing venation of Hepialoidea: A, *Palaeoses*, Palaeosetidae; B, *Anomoses*, Anomosetidae; C, *Fraus*, D, *Oncopera*, Hepialidae.

[T. Binder, R. Nielsen, J. Wedgbrow]

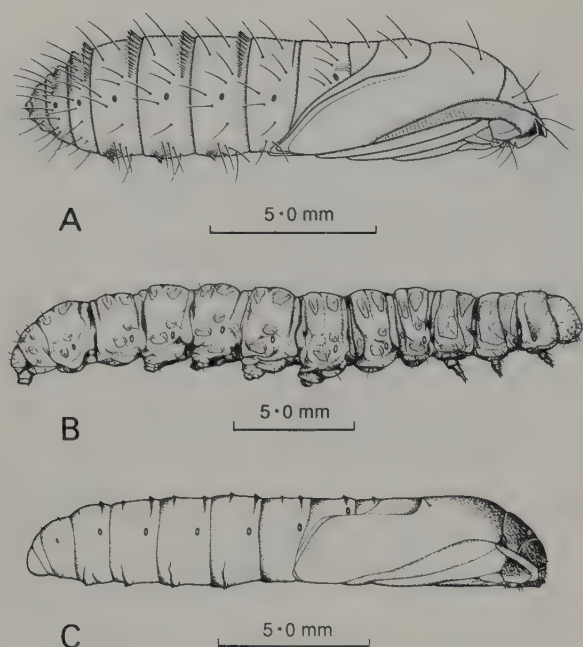


Fig. 41.21 Hepialidae: A, pupa of *Fraus*; B, C, larva and pupa of *Aenetus*.  
[T. Binder, S. P. Kim, J. Wedgbrow]

spurs 0-2-4; wings devoid of microtrichia beyond base, with both primitive- and normal-type scales, jugum and frenular bristles present; fore wing (Fig. 41.20B) with prominent tuft of erect, spatulate scales at base, with Sc forked,  $R_4$  and  $R_5$  stalked or free, CuP present; hind wing with pencil of hair-scales in long pocket formed by a fold of inner portion of dorsum.

The family is endemic to Australia. It contains only *Anomoses hylecoetes* (Fig. 41.17G), which has been placed in its own family by Turner (1922) and Kristensen (1978b) or in the otherwise southern African family Prototheoridae (Philpott 1928). *A. hylecoetes* is a dull brown moth from rainforests in southern Qld and northern N.S.W. It comes to light and has been collected in Malaise traps during the spring and early summer. Nothing is known about the immature stages or their life history.

**6. Hepialidae** (ghost moths, swifts). There is now evidence that the Hepialidae as treated in the 1st edition are not monophyletic. However, the family assignment of *Fraus* and three other genera is undetermined and they are here treated in the informal grouping 'primitive Hepialidae' and the remaining Hepialidae as the Hepialidae *s. str.*

'PRIMITIVE HEPIALIDAE' (Figs 41.17H, I). Small to medium-sized; head with lamellar or piliform scales; flagellar segments bipectinate or each with one rounded lobe; mandibles small to vestigial; proboscis short or absent; maxillary palps 1-segmented; labial palps 2- or 1-segmented; epiphysis present or absent; spurs absent; hind tibia not modified; wings aculeate, with only normal-type scales, scales with larger tooth at each distal corner; fore wing (Fig. 41.20C) with Sc simple,  $R_2+R_3$  and  $R_4$  and  $R_5$  stalked (cross-vein R-M<sub>1</sub> reaches  $R_{4+5}$  between furcation

$R_{2+3}/R_{4+5}$ ), CuP present in basal half of wing; female hind wing with weak hair-pencil. Pupa with one transverse row of spines on T3 to T6 (Fig. 41.21A).

*Fraus*, endemic to Australia, and three non-Australian genera (*Afrotheora*, *Antihepialus* and *Gazoryctra*) were excluded from the Hepialidae in order to make that group monophyletic (Nielsen and Scoble 1986). *Fraus* (25 spp.) occurs in eastern and southern Australia. All but one of the species fly from late January to late June. *F. orientalis* (Fig. 41.17H) is common along the east coast and is typical of several species with slender, longitudinally striped wings and slender body. *F. simulans*, a minor pest of pastures in Tas., has a wide range in southern Australia, and is typical of the heavy-bodied *Fraus* species without proboscis and epiphysis; its larva constructs a silk-lined vertical tunnel in the soil and feeds at night, mainly on adjacent grasses (Hardy 1973). The similar *F. polyspila* (Fig. 41.17I) is locally extremely abundant in southern, mainland Australia. Flight takes place shortly after sunset; one species, *F. fusca*, flies during the afternoon at higher altitudes (Nielsen and Kristensen 1989).

HEPIALIDAE *s. str.* (Plate 8, A; Figs 41.17J-L). Medium-sized to very large; head with piliform scales; flagellar segments angular, dentate, bipectinate, tripectinate or simply cylindrical; proboscis absent; maxillary palps minute, 1- or 2-segmented; epiphysis present or absent; spurs absent in all Australian species; hind tibia with prominent hair-pencil in some species; wings aculeate, with only normal-type scales; fore wing (Fig. 41.20D) with Sc simple or forked;  $R_2$  and  $R_3$  stalked,  $R_4$  and  $R_5$  separate beyond cross-vein R-M in Australian species or  $R_4$  and  $R_5$  from stem of  $R_{2+3}$  (oxycanus-type venation). Egg nearly spherical, surface without ribs, with two micropyles. Larva (Fig. 41.21B) long, cylindrical, with 6 stemmata, 3-segmented maxillary palps, thoracic legs and abdominal prolegs present, crochets in multiserial ellipse. Pupa (Fig. 41.21C) long, cylindrical, with rudimentary mandibles, maxillary palps absent; appendages fused to body wall, abdominal terga each with 2 transverse rows of spines and S7 with ventral transverse row of spines (often connected to anterior dorsal row on T7); segments 3-7 in males and 3-6 in females movable; cremaster absent.

The Hepialidae *s. str.* are richly represented in Australia and include many large species. *Zelotypia* (1 sp.) and *Aenetus* (16 spp.) contain beautiful species, whose larvae tunnel down vertically in the stems of living trees and shrubs. They feed on the bark regrowth around the entrance to the tunnel, where they form a vestibule covered with a webbing of silk, wood particles and faecal pellets. Pupation occurs in the tunnel, the entrance being previously closed with a silken wad. The larvae of the large, orange-brown *Z. stacyi* (Fig. 41.17J) tunnel in *Eucalyptus* in southern Qld and eastern N.S.W. Most *Aenetus* species are strongly sexually dimorphic. *A. ligniveren* is a relatively small species from the coast and tablelands in south-eastern Australia; its larvae make a relatively short tunnel in various small trees, including *Eucalyptus*, *Acacia* and *Lantana*. *A. eximia* (Plate 8, A) is larger and its larvae often make tunnels 50 cm long in the



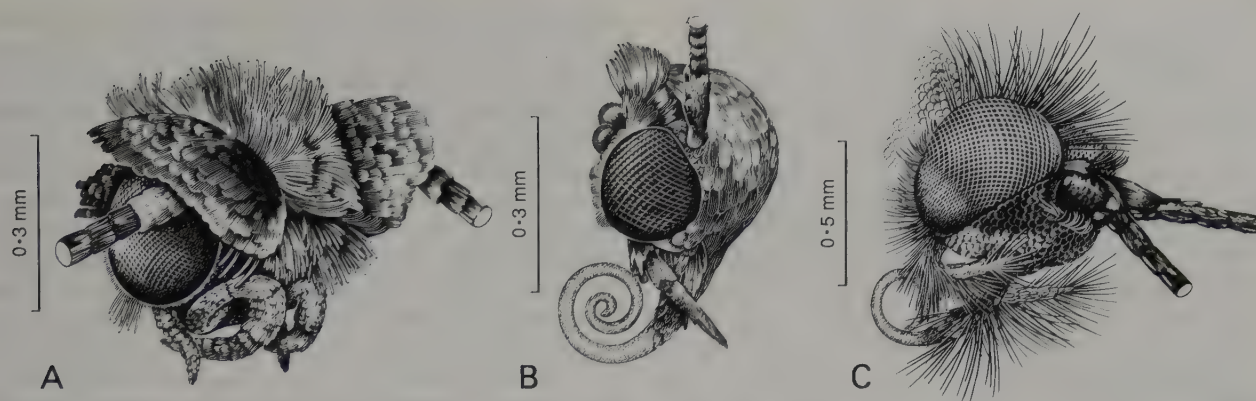


Fig. 41.22 Heads: A, *Pectinivalva*, Nepticulidae; B, *Heliozela*, Heliozelidae; C, *Nemophora*, Adelidae.

[F. Nanninga]

stems and roots of *Acmena*, *Prostanthera* and other trees. *A. dulcis* is a large species with white males and green females from south-western W.A. with larvae in *Agonis*. The larvae of several *Aenetus* species are sought by black cockatoos.

Larvae of *Oncopera* (12 spp.) form vertical tunnels in the soil; the larvae emerge at night to feed on the foliage of herbaceous plants growing near the entrance to the tunnel; others feed on leaf litter on the ground in rainforest. A few species are serious pasture pests in southern Australia. The larvae of *Trictena* (3 spp.) and *Abantiades* (14 spp.) live in vertical tunnels in the soil and feed externally on the roots of *Eucalyptus* and other trees. Their life history is well adapted to the aridity of inland Australia, where great flights of the moths occur after a fall of rain. Natural mortality of the early stages is very high; a single female of *A. magnificus* (Fig. 41.17k) lays more than 18 000 eggs. *Oxycanus* (44 spp.) (Fig. 41.17l) is the largest Australian genus and has, like *Elhamma* (1 sp.) and *Jeana* (2 spp.), oxycanus-type venation. The larvae of *Oxycanus* live in vertical tunnels rather similar to *Oncopera*. The species may be very common locally, and

a few are pasture pests, while others feed on leaf litter on the soil surface or externally on *Acacia* roots. The flight of several *Oxycanus* species is, often spectacularly, correlated with rain. [Common 1966a; Hardy 1974; Tindale 1932–64]

### Infraorder HETERONEURA

This entity comprises the monotrysian heteroneuran grade (sometimes called Monotrysia (D. R. Davis 1986)) and the Ditrysia. Remarkable autapomorphies include heteroneurous venation and retinaculo-frenulate wing coupling and unsclerotised abdominal S1.

### Superfamily NEPTICULOIDEA

Very small; ocelli and chaetosemata absent; antennae with scape expanded and concave forming eye-cap, flagellum with specialised sensilla; fore tibial epiphysis absent; tibial spurs 0–2–4; hind tibiae with prominent spines; wings with microtrichia, at least at base, both wings with venation specialised (reduced); wing coupling modified; ovipositor non-piercing, blunt. Pupa protruded from oval cocoon at ecdysis.

### Key to the Families of Nepticuloidea Known in Australia

- Wing coupling effected by pseudofrenular bristles curved around vein M of fore wing ..... **Opostegidae** (p. 842)  
 Wing coupling effected by frenulum hooked into costal retinaculum of curved spines and pseudofrenular bristles of hind wing ..... **Nepticulidae** (p. 841)

**7. Nepticulidae** (Fig. 41.26A). Head (Fig. 41.22A) with erect hair-scales and characteristic 'collar' on back of head of either lamellar or piliform scales; antennae with highly specialised, paired sensilla vesiculoclada (van Nieukerken and Dop 1987); fore wing (Fig. 41.23A) with M and R coalescent except terminally, R usually 4-branched, M one- or two-branched; wings of males often with specialised scales on underside of fore wing and both sides of hind wing. Egg oval, flattened, convex. Larva without segmented thoracic legs or crochets; pseudolegs ('calli') often present on meso- and metathorax and on first 7 abdominal segments; head with a single stemma on each side; abdominal segment 10 with pair of internal sclerotised rods. Pupa with appendages not glued

to body, 3 pairs of coxae visible, abdominal segments 2–7 movable; T2–8 with numerous spines.

Only 16 species of Nepticulidae have been described from Australia. They are, however, numerous and the fauna may well exceed 300 species. Most Australian species are black, but some are brown or grey, or have a transverse, silvery fascia (Fig. 41.26A) typical of many species in the Northern Hemisphere. The family has been intensively studied in many parts of the world (van Nieukerken 1986). The adults often fly around their host plants during the day, come to light at night and are often seen running rapidly over leaves of the host plant. The larva tunnels direct from the egg into the leaf, forming a slender, tortuous mine, which later expands gradually or

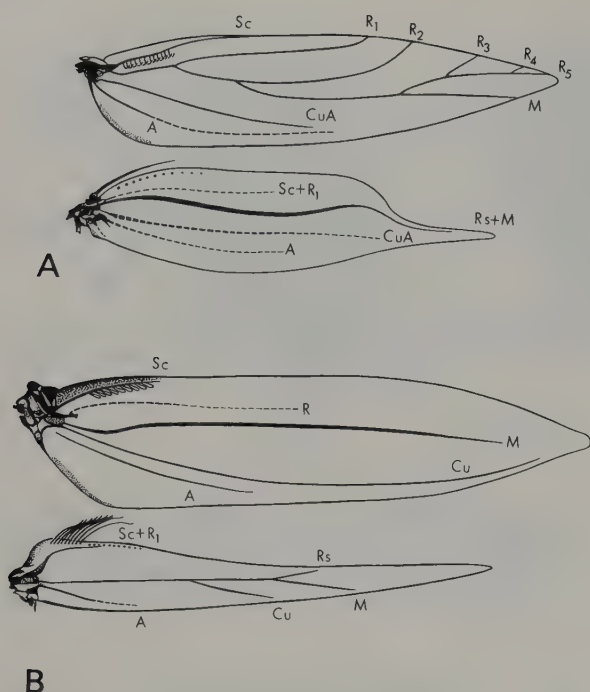


Fig. 41.23 Wing venation of Nepticuloidea: A, *Pectinivalva*, Nepticulidae; B, *Opostega*, Opostegidae. [T. Binder]

abruptly into a blotch mine. The form of the mine and the host plant are often characteristic of the species. At maturity the larva normally leaves the mine and spins an oval cocoon of silk on the ground; pupa (Fig. 41.25A).

**PECTINIVALVINAE.** Subdorsal retinaculum absent; 1A+2A not thickened in fore wing; trunk Rs+M deflected towards costa in hind wing; valva with rows of blunt spines, pectinifer. The subfamily is endemic to Australia with many species in the one genus *Pectinivalva*. The larvae are leaf-miners in the myrtaceous genera *Callistemon*, *Eucalyptus* and *Lophostemon* (Scoble 1983).

**NEPTICULINAE (Stigmellinae).** Subdorsal retinaculum usually present in both sexes; 1A+2A thickened in fore wing; trunk Rs+M not deflected towards costa in hind wing; valva without pectinifer.

*Stigmella* is probably the largest Australian genus of this subfamily. Mines are known from a wide range of host plants; one species mines *Acacia phyllodes*.

**8. Opostegidae** (Fig. 41.26B). Head with tuft of long,

hair-like scales between antennae and on vertex; antennae with expanded eye-caps and special, branched sensilla (similar to ascoid sensilla in Micropterigidae) on flagellar segments (van Nieukerken and Dop 1987); labial palps drooping; wing coupling in both sexes by long, curved pseudofrenular bristles curving around ventrally expanded M vein in fore wing (Nielsen 1985a); fore wing with 4 or 5 unbranched veins (Fig. 41.23B); valva with pectinifer. Larva apodous, long, very slender and nematode-like; head with single rudimentary stemma on each side. Pupa in general form similar to that of Nepticulidae, scape of antenna nearly covering eye, 3 pairs of coxae visible.

Adults are usually white with dark pattern. Australia has a rich fauna of which 19 are named. Some Australian species with a wingspan of 15 mm are among the largest in the family. The family contains few genera. One Australian species belongs to an unnamed genus, while all others are placed in *Opostega*. The biology of Australian species is unknown, but elsewhere opostegid larvae either mine in leaves or excavate mines up to 1 m long in cambium. Adults fly in the late afternoon and come to light. [D. R. Davis 1989]

### Superfamily INCURVARIOIDEA

Incurvarioidea (Adeloidea) are small to very small; ocelli and chaetosemata absent; antennae short to markedly longer than fore wing, scape without eye-cap, often with pecten; proboscis long, short or absent, scaled near base; maxillary palps 5-segmented to reduced; labial palps 3-segmented (rarely absent), second segment with lateral bristles; epiphysis usually present; tibial spurs 0-2-4 (rarely 0-2-2); wings usually with microtrichia, hind wing usually with frenulum and pseudofrenular bristles; male often with rows of blunt spines (pectinifers) on valva and with arrow-shaped juxta; female with long vestibulum supported by strong muscle tendons ('guy wires') and piercing ovipositor for inserting eggs in plant tissues. Larva apodous or with short prolegs, crochets in transverse rows, anal prolegs and crochets usually absent; leaf-miners later cutting out or forming flattened cases used as portable shelters while leaf-skeletonising or feeding on flowers or for pupation, or gall-makers or internal borers in stems and twigs. Pupa protruded from case at ecdysis.

The superfamily contains six families (Nielsen and Davis 1985) of which Crinopterygidae, Cecidosidae and Prodoxidae (which include the North American yucca moths) are not recorded from Australia.

#### Key to the Families of Incurvarioidea Known in Australia

1. Antennae longer than fore wing ..... **Adelidae** (p. 843)
- Antennae shorter than fore wing ..... 2
- 2(1). Head smooth-scaled (Australian species); hind wing without cross-vein M-CuA (cell open) ..... **Heliozelidae** (p. 842)
- Head rough-scaled; hind wing with cross-vein M-CuA (cell closed) ..... **Incurvariidae** (p. 844)

**9. Heliozelidae** (Figs 41.26C, D). Small to very small, wingspan 3.0 mm in smallest Australian species; head (Fig. 41.22B) smooth-scaled in all Australian species, often shining; labrum usually without spinose pilifers; antennae short; proboscis long, longer than labial palps; maxillary palps minute, 5-segmented or reduced; fore

wing (Fig. 41.24A) with or without microtrichia, 1A+2A coalescent from base in all Australian species; hind wing without cross-vein M-CuA, pseudofrenular bristles often modified. Larva apodous in all instars, prolegs on segments 4-6 sometimes represented by crochets; head with 2 stemmata on each side. Pupa with appendages not glued



to body, maxillary palps absent, abdominal terga with fine dorsal spines.

The moths, which often have metallic scales, fly in sunshine and rest on flowers. The larvae are leaf- and petiole-miners in trees and shrubs, finally cutting out flat, oval cases from the mine, which either drop to the ground or are attached on the host or elsewhere before pupation. *Hoplophanes* (Fig. 41.26C) (20 spp.), with wingspan up to 16 mm, contains the largest heliozelids. *Heliozela* (Fig. 41.26D), with many Australian species, often mines young terminal leaves of *Eucalyptus*. *Antispila*, with few species in eastern Australia, mines leaves of *Cissus*.

**10. Adelidae** (Plate 7, I; Fig. 41.26E). Head (Fig. 41.22C) with raised hair-scales; compound eyes often large and sometimes almost holoptic in males. Adelids have the longest antennae in the Lepidoptera; antennae longer than fore wing in all Australian species, 2 to 5 times length of fore wing in males, often shorter in females; proboscis long to very long, scaled at base; fore

wing with chorda well developed (Fig. 41.24B); tip of ovipositor slender and almost pointed. Larva in case in flowers or in case among leaf litter. Pupa (Fig. 41.25B) with appendages at most lightly glued to body, maxillary palps present, long antennae wrapped around abdomen.

**NEMATOPOGONINAE.** Compound eyes normal; antennae of similar length in male and female, males without specialised pegs on flagellum; antennae bent backwards in repose; maxillary palps long, almost as long as proboscis, 4- or 5-segmented; labial palps with moderate lateral bristles; fore wing greyish without metallic coloration,  $R_5$  to termen well below apex. The adults are nocturnal and the larvae live in portable cases in leaf litter. A mainly temperate group. *Ceromitia* (Fig. 41.26E) (10 spp.) occurs in southern Australia and has its closest relatives in South America and southern Africa. [Nielsen 1985c]

**ADELINAE.** Compound eyes large in males (Fig. 41.22C); antennae markedly longer in male than female, males with prominent pegs on proximal flagellar seg-

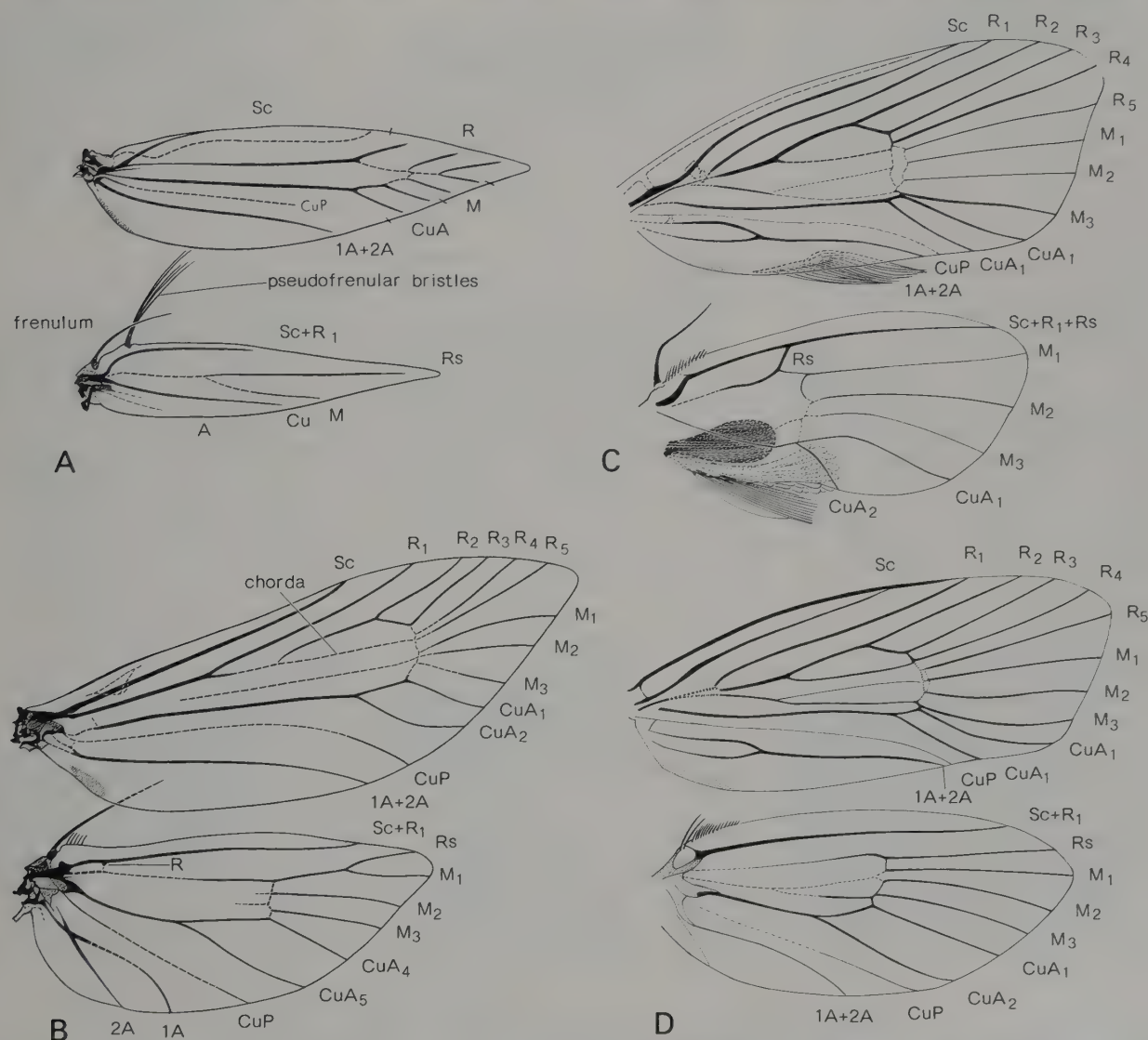


Fig. 41.24 Wing venation of Incurvarioidea and Palaephatoidea: A, *Heliozela*, Heliozelidae; B, *Nemophora*, Adelidae; C, D, *Azaleodes*, ♂, ♀, Palaephatoidea. [A, B by T. Binder; C, D by A. Hastings]

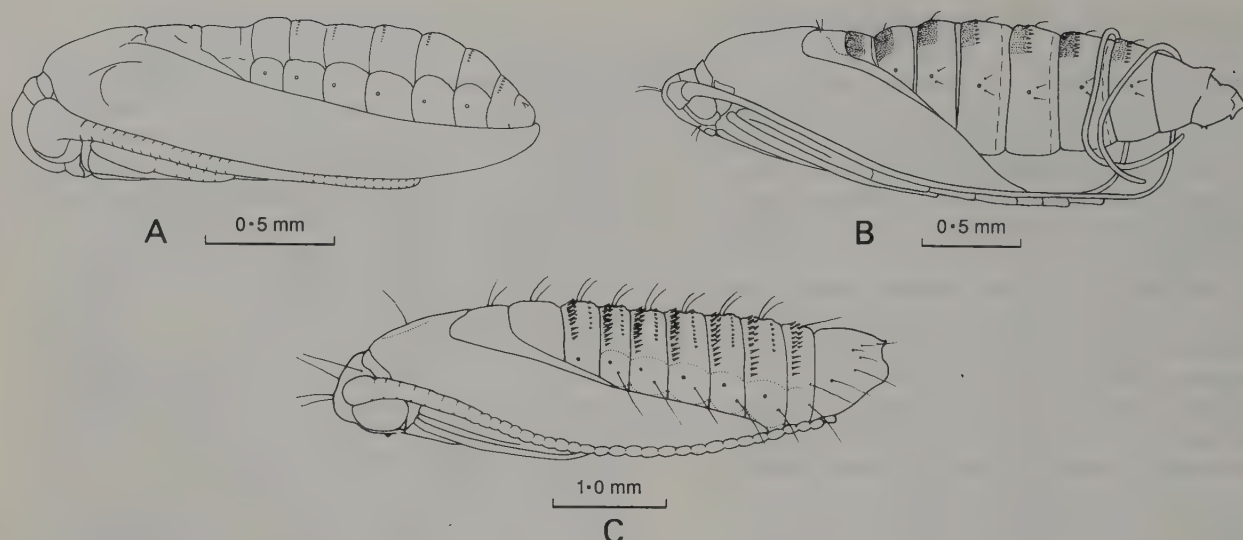


Fig. 41.25 Pupae: A, *Stigmella*, Nepticulidae; B, *Nemophora*, Adelidae; C, *Perthida*, Incurvariidae.

[I. F. B. Common]

ments; antennae extended upwards in repose; maxillary palps short, 2- or 3-segmented, about one-tenth length of proboscis; labial palps strongly setose; fore wing with brilliant metallic coloration (Plate 7, I),  $R_5$  to costa. The adults fly in sunshine and males of some species swarm; both sexes rest on flowers. The larvae feed on flowers of *Acacia* and later form a case from flower parts and feed on fallen flowers on the ground; the larvae of another species are found in cases within the dry seed capsules of *Bursaria* flowers. A mainly tropical group with *Nemophora* (10 spp.) in Australia.

**11. Incurvariidae** (Fig. 41.26F). Small; head with raised hair-scales; antennae to about mid length of fore wing; proboscis short, unscaled; maxillary palps 5-segmented; labial palps with lateral bristles on second segment; fore tibia without epiphysis in several genera; Australian species sombre coloured, sometimes with white marks, without metallic lustre. Ovipositor flattened, triangular, piercing. Larva with 6 stemmata, thoracic legs and prolegs present or absent, crochets when present in transverse row. Pupa (Fig. 41.25C) with appendages not glued to body, maxillary palps present.

The family reaches its greatest diversity in Australia with 5 genera and more than 100 species. The larvae feed on trees and shrubs of the families Proteaceae and Myrtaceae. Some are leaf-miners throughout life and, when mature, cut a flat case from the mine for pupation. Others mine at first and then cut out increasingly large cases which they use as shelter when feeding within a new mine or when browsing on the leaf surface. Pupation takes place in the case, on the ground or attached to the food plant. *Perthida* (Fig. 41.26F), with more than 30 species, is the largest Australian genus and includes pest species on jarrah (*Eucalyptus marginata*) and other eucalypts (Common 1969). Two other genera feed on *Eucalyptus*, including one which cuts irregular, flimsy cases from successively larger, irregular mines on leaves of seedlings. A large genus has larvae leaf-mining various *Banksia* species; the closest relative of this genus and

another Australian Proteaceae-feeding genus is a South African genus leaf-mining in *Protea*.

### Superfamily PALAEPHATOIDEA

**12. Palaephatidae** (Figs 41.26G, H). Small to very small; head with raised piliform scales; ocelli present or absent; pilifers setose; proboscis present, maxillary palps 5- (or rarely 4-) segmented; labial palps with lateral bristles on second segment; epiphysis present; spurs 0-2-4; wings with microtrichia (sometimes absent on base of fore wing), scales with ridge dimorphism, fore wing (Fig. 41.24D) usually with all R and M veins separate; fore and hind wings and abdomen of males often with hair-pencils and specialised scales (Fig. 41.24C); ovipositor non-piercing, short and nearly truncate, with medial sensory ridge; ductus bursae often with a complex sclerotised structure posteriorly (colliculum). Pupa with one transverse row of spines anteriorly on abdominal terga.

Five genera and 28 species of this family occur in southern South America (D. R. Davis 1986) and two genera and about 30 species in Australia. The species of *Azaleodes* (Fig. 41.26H; 4 spp.) are strongly sexually dimorphic (Nielsen 1987). *Azaleodes* and some species of *Ptysoptera* (25 spp.) occur in rainforests in eastern Australia. Other species of *Ptysoptera* (Fig. 41.26G) are widely distributed in Australia; larvae feed on *Perseonia* and other Proteaceae, at first mining in leaves and later living in shelters formed by joining adjacent leaves.

### Series DITRYSIA

The monophyly of the Ditrysia, which contains 98% of all Lepidoptera, is not in question. All Ditrysia share ditryisian genitalia and the adult S2 has a pair of anterior apodemes. The distribution of such important novelties as primary and secondary oblique proboscis muscles and the presence of abdominal sex pheromone glands, both of which occur widely in the Ditrysia, is not known well enough to establish whether these and certain other ditryisian features are indeed ditryisian autapomorphies (Nielsen 1989).



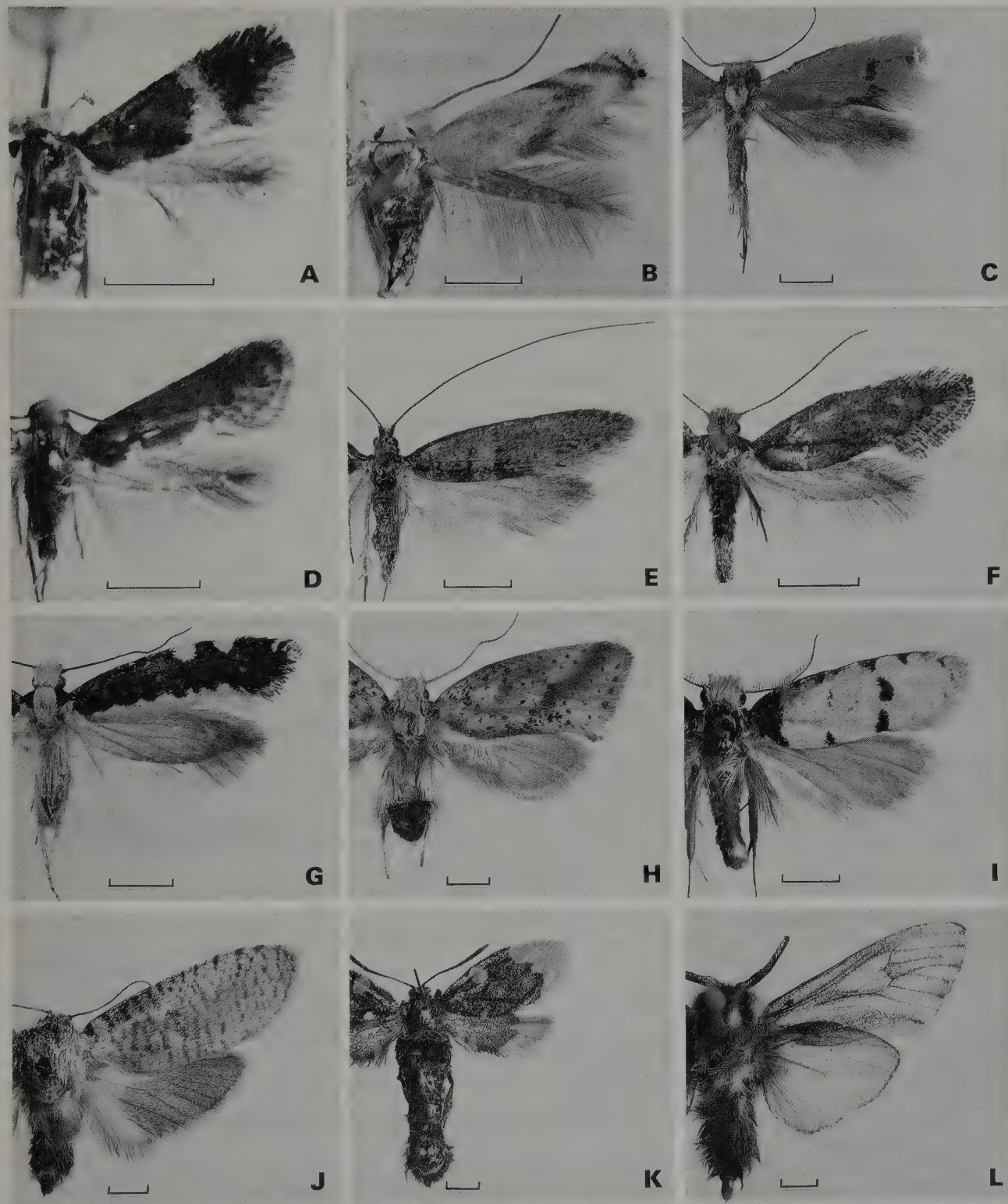


Fig. 41.26 A, *Stigmella anazona*, Nepticulidae; B, *Opostega gephyraea*, Opostegidae; C, *Hoplophanes chlorochrysa*, D, *Heliozela prodela*, Heliozelidae; E, *Ceromitia iolampra*, Adelidae; F, *Perthida* sp., Incurvariidae; G, *Ptyssoptera* sp., H, *Azaleodes micronipha*, Palaephatidae; I, *Ip hierga macarista*, J, *Trigonocyttara clandestina*, K, *Cebysa leucotelus*, L, *Clania tenuis*, Psychidae. Scales = 2 mm.  
[J. Green, C. Lourandos]

*Key to the Superfamilies of Ditrysia Known in Australia*

The following is a tentative key utilising readily observable, external features. It is not possible to provide a reliable key to the ditrysiian superfamilies without including the structure of the genitalia and skeletal anatomy. Keys to the ditrysiian families are given by J. D. Holloway (1986), Holloway *et al.* (1987) and Dugdale (1988b).

1. Proboscis scaled ..... 2
- Proboscis unscaled or absent ..... 4
- 2(1). Labial palps recurved, apical segment may exceed vertex, usually tapering; chaetosemata absent, S2 of tineid type (p. 847); tympanal organs absent ..... GELECHIOIDEA (p. 859)
- Labial palps porrect, beak-like or ascending; chaetosemata present or absent; S2 of tortricoid type (p. 870); tympanal organs present at base of abdomen or absent ..... 3
- 3(2). Labial palps ascending; fore wing with CuP present near termen; tympanal organs absent ..... SESIOIDEA (pt, p. 874)
- Labial palps porrect, beak-like, or ascending; CuP usually absent; tympanal organs present at base of abdomen ..... PYRALOIDEA (p. 886)
- 4(1). Antennae gradually or abruptly clubbed, tip sometimes hooked ..... 5
- Antennae filiform or tapered, often ciliate, pectinate or plumose ..... 7
- 5(4). Hind wing with frenulum; ocelli present, large; chaetosemata absent ..... CASTNIOIDEA (p. 874)
- Hind wing usually without frenulum; ocelli absent; chaetosemata present ..... 6
- 6(5). Antennae widely separated at base; with subapical thickening; fore wing with all veins from discal cell arising separately ..... HESPERIOIDEA (p. 893)
- Antennae approximated at base, with apical thickening; fore wing usually with at least some peripheral veins stalked ..... PAPILONOIDEA (p. 895)
- 7(4). Tympanal organs present in thorax or abdomen (Figs 41.6, 7) ..... 8
- Tympanal organs absent ..... 13
- 8(7). Tympanal organs in metathorax, counter-tympanal cavities usually at base of abdomen ..... NOCTUOIDEA (p. 905)
- Tympanal organs in abdomen ..... 9
- 9(8). Chaetosemata absent ..... 10
- Chaetosemata present ..... 12
- 10(9). Fore wing broad, usually falcate ..... DREPANOIDEA (p. 891)
- Fore wing narrow, not falcate ..... 11
- 11(10). Fore wing reddish brown, with silvery marks ..... COSSOIDEA (pt, p. 870)
- Fore wing grey ..... TINEOIDEA (pt, p. 847)
- 12(9). Fore wing with R veins combined in one branching system; areole often present; hind wing rarely with tails; tympanal organ in both sexes in S2 ..... GEOMETROIDEA (p. 889)
- Fore wing with R<sub>5</sub> remote from R<sub>1</sub>-R<sub>4</sub> and usually stalked with M<sub>1</sub>; areole absent; hind wing usually with tail; tympanal organ in ♂ between S2 and S3, in ♀ in S2 ..... URANIOIDEA (p. 892)
- 13(7). Wings deeply cleft into two or more plumes ..... 14
- Wings not cleft ..... 15
- 14(13). Hind wing divided into 3 plumes ..... PTEROPHOROIDEA (pt, p. 883)
- Hind wing divided into 6-7 plumes ..... ALUCITOIDEA (pt, p. 882)
- 15(13). CuP absent as a tubular vein in fore wing ..... 16
- CuP well developed, at least near margin, as a tubular vein in fore wing ..... 22
- 16(15). Head vestiture of piliform scales; robust, medium-sized to very large species ..... 17
- Head vestiture of lamellar scales; small to medium-sized species ..... 18
- 17(16). Body long and fusiform; wings narrow, termen very oblique; proboscis usually well developed, often long ..... SPHINGOIDEA (p. 904)
- Body often stout but not fusiform; wings broad, termen not unusually oblique; proboscis often reduced ..... BOMBYCOIDEA (p. 899)
- 18(16). Hind wing CuA with pecten; fore wings often with raised scales ..... COPROMORPHOIDEA (pt, p. 880)
- Hind wing CuA without pecten; fore wing without raised scales ..... 19
- 19(18). Abdominal terga with anterior band of spines; S2 with V-shaped sclerotisation ..... ALUCITOIDEA (pt, p. 882)
- Abdominal terga without spines; S2 without V-shaped sclerotisation ..... 20
- 20(19). Labial palps beak-like; ♂ hind tibia with apical lobe and hair-pencil; fore wing with 2A sinuous ..... HYBLAEIOIDEA (p. 885)
- Labial palps not beak-like; ♂ hind tibia without apical lobe; 2A in fore wing not sinuous ..... 21
- 21(20). Wing long and narrow, not with netted pattern; fore wing without 1A+2A fork; hind wing with specialised scales on underside ..... PTEROPHOROIDEA (pt, p. 883)
- Wings broad with fine, netted pattern; fore wing with 1A+2A fork; hind wing without specialised scales on underside ..... THYRIDOIDEA (p. 885)
- 22(15). S2 of tineid type (S2 apodemes long and slender); usually small to very small delicate species, usually without raised scales on fore wing ..... 23
- S2 of tortricoid type (S2 apodemes short and broad); usually robust, small to very large species; sometimes with raised



- scales on fore wing ..... 24
- 23(22). Abdominal segment 8 of ♂ with prominent lobes; fore wing with  $R_5$  often to termen and M usually absent from discal cell ..... YPONOMEUTOIDEA (p. 854)
- Abdominal segment 8 of ♂ without lobes; fore wing with  $R_5$  often to costa; M usually present in discal cell ..... TINEOIDEA (pt, p. 847)
- 24(22). Fore wing with raised scales on surface or along dorsum ..... 25
- Fore wing without raised scales ..... 26
- 25(24). Fore wing with raised scales along dorsum; wing narrow, almost parallel sided ..... EPERMENIOIDEA (p. 881)
- Raised scales on fore wing not restricted to dorsum; wing relatively narrow, rectangular ..... COPROMORPHOIDEA (pt, p. 880)
- 26(24). Chaetosemata present; ocelli absent; fore wing without chorda and M stem in cell ..... IMMOIDEA (p. 880)
- Chaetosemata present or absent; ocelli present or absent; fore wing usually with both chorda and M in cell ..... 27
- 27(26). Lower part of frons with ascending scales; ocelli and chaetosemata present; ovipositor lobes leaf-like ..... TORTRICOIDEA (p. 873)
- Lower part of frons without ascending scales; ocelli and chaetosemata rarely both present; ovipositor lobes not leaf-like ..... 28
- 28(27). M tubular and forked in cell; chaetosemata absent ..... COSSOIDEA (pt, p. 870)
- M absent from cell or M not present in cell as a complete, forked, tubular vein; chaetosemata present or absent ..... 29
- 29(28). CuP in fore wing a well developed tubular vein ..... ZYGAENOIDEA (p. 877)
- CuP in fore wing weak or only present as a tubular vein at margin ..... SESIOIDEA (pt, p. 874)

### Superfamily TINEOIDEA

Very small to medium sized; ocelli present or absent; chaetosemata absent; scape sometimes forming eye-cap; proboscis present, naked or reduced; maxillary palps 1- to 5-segmented, folded, porrect or ascending, not folded over base of proboscis; labial palps usually short, drooping or ascending, sometimes with lateral bristles, apical segment usually not acute; epiphysis rarely absent; spurs 0-2-4, rarely reduced;  $R_5$  often to costa, M retained in discal cell and CuP strong in primitive forms, venation often reduced, especially in hind wings of narrow-winged species; abdomen without dorsal spining; S2 of tineid type (S2 apodemes long, slender and connected to sternal rods); ovipositor usually with additional ventral 'apophyses'. Larva with 3 prespiracular (L) setae on prothorax (only 2 in Scardiinae); crochets, when present, in circle, ellipse, penellipse or transverse band, setae L1 and L2 of abdomen often remote; concealed feeders, in portable

cases, tunnels, silken tubes, and leaf mines. Pupa with dorsal abdominal spines, in male usually with segments 4-7, 4-8 or 5-8 movable; in larval shelter or silken cocoon, except for some female Psychidae protruded from cocoon or shelter at ecdysis.

This is probably the most primitive of the non-apoditrypsian superfamilies (Fig. 41.13B). Archaic forms retain M in the discal cell, have only a slightly reduced heteroneurous venation, and sometimes have 5-segmented, folded maxillary palps. The reduced mouth-parts in the Psychidae, the reduced venation in small, narrow-winged Gracillariidae and Bucculatricidae are specialised conditions.

There is little evidence for the monophyly of the Tineoidea but the superfamily can be divided into two groups of families each of which is believed to be monophyletic (G. S. Robinson 1989; D. R. Davis (1988) formally named these groups Tineoidea and Gracillarioidea.

### Key to the Families of Tineoidea Known in Australia

1. With prominent ocelli ..... **Douglasiidae** (p. 852)
- Without ocelli (Australian spp.) ..... 2
- 2(1). Proboscis elongate and rolled, the two galeae completely associated ..... 3
- Proboscis short, vestigial, or absent, the two galeae disassociated at least for some of the proboscis length ..... 5
- 3(2). Antenna considerably shorter than fore wing, flagellum scaled only on dorsal surface ..... **Galacticidae** (p. 851)
- Antenna as long as or longer than fore wing, flagellar segments completely scaled ..... 4
- 4(3). Antenna with flagellar segments each bearing one row of scales; cilia of hind wing longer than breadth of wing ..... **Gracillariidae** (p. 852)
- Antenna with flagellar segments each bearing two rows of scales; cilia of hind wing shorter than breadth of wing ..... **Roeslerstammiidae** (p. 851)
- 5(2). Antennal scape with eye-cap ..... **Bucculatricidae** (p. 851)
- Antennal scape without eye-cap ..... 6
- 6(5). Antenna with flagellar segments each bearing a single row of scales; fore wing with  $R_5$  to costa or apex; ♂ retinaculum arising from Sc; ♀ frenulum with three or fewer bristles ..... **Tineidae** (p. 848)
- Antenna with flagellar segments each bearing two rows of scales, or with scales scattered or absent; fore wing with vein  $R_5$  to termen; ♂ retinaculum arising from membrane anterior to Sc; ♀ frenulum, if present, of 5 or more bristles ..... 7
- 7(6). Labial palps with lateral bristles; antennal scape with pecten; proboscis present ..... **Eriocottidae** (p. 848)
- Labial palps without lateral bristles; antennal scape without pecten; proboscis vestigial or absent ..... **Psychidae** (p. 848)

**13. Psychidae** (Figs 41.26I–L). Small to medium sized; head with roughened hairs; ocelli present or absent; antennae often bipectinate to apex; proboscis and maxillary palps rudimentary or absent; labial palps short or rudimentary, without lateral bristles; epiphysis usually present, sometimes very long; tibial spurs 0-2-4, 0-1-1 or absent; fore wing (Figs 41.27A–C) with M usually present in discal cell, often forked, chorda sometimes present; CuP usually separate or partly fused with 1A+2A or connected by a cross-vein; hind wing with M usually present in discal cell, sometimes forked,  $R_1$  sometimes joining  $R_s$  and  $Sc$ , sometimes one or more short branches from  $Sc+R_1$  to costa, CuP often present; females fully winged, brachypterous or apterous; abdomen in male often grossly extensible, in female with anal tuft of long hair. Larva case bearing; case with anterior opening through which larva feeds, and posterior opening through which faecal pellets are ejected (Fig. 41.33); crochets in lateral penellipse, uniordinal. Pupa (Figs 41.31A, B) with dorsal abdominal spines, in female eyes and appendages sometimes greatly reduced or absent; in larval case, partially protruded at ecdysis or, in females of some species, remaining in case.

Australia is rich in primitive species, often with fully-winged females, sometimes referred to the TALEPORIINAE. They have relatively simple venation, with M usually present and often forked in the discal cell of both wings. The fore wings often lack one vein, and the tibial spurs are 0-2-4. The larvae feed on many angiosperms, but a few feed on gymnosperms, lichens and mosses. Certain exotic species feed on dead insects.

*Ctenocompa* (1 sp.) and *Trigonocyttara* (1 sp.) have winged females. The larva of the stout-bodied *T. clandestina* (Fig. 41.26j) forms a cylindrical case (Fig. 41.33D) with one or two twigs attached lengthwise. It feeds on *Eucalyptus*, *Acacia*, the introduced *Pinus radiata*, and several exotic ornamentals. In *Lepidoscia arctiella* the female has vestigial wings, but emerges normally from the pupal cuticle which, as in the males of all species, partially protrudes from the larval case at ecdysis. Fertilisation takes place near or on the slender, tapering case (Fig. 41.33B), which is ornamented with spirally-arranged short lengths of twig. The brilliant metallic green and orange female of *Cebysa leucotelus* (Fig. 41.26k) has short, non-functional wings. An unfertilised female soon attracts several eagerly fluttering males, even in bright sunshine. The larvae form soft sacks (Fig. 41.33A) tapering at each end and ornamented with tiny pieces of the lichens upon which the larvae feed.

*Ardiosteres* (10 spp.), with dentate antennae, and *Iphiherga* (Fig. 41.26i; 12 spp.), with bipectinate antennae, have both been referred to the Tineidae but belong to the Psychidae. However, they cannot yet be assigned to a subfamily. They often have transverse wing patterns in black and white or black and orange. The 2nd segment of the labial palp has long projecting scales, but lacks bristles. The case-bearing larvae of *I. macarista* occur in meat ant nests, and are thought to be scavengers.

In the more specialised PSYCHINAE (Turner 1947) the males have short, thinly-scaled wings and fly rapidly. The

enlarged costal area of the hind wing is usually strengthened by one or more short branches from  $Sc+R_1$ . Females are apterous and the legs are greatly reduced. They are fertilised within the larval case, and the eggs, mixed with hair shed from the tip of the female abdomen, are laid within the pupal cuticle, from which the female usually partially, but sometimes completely, emerges in the process. Spent females sometimes drop from the lower opening of the case, through which the young larvae later descend on silken threads. In some species wind drift of larvae suspended from strands of silk greatly aids dispersal. Larvae at first run rapidly on their thoracic legs, with the abdomen held high in the air. Later they construct a small conical case, which is gradually enlarged as they grow.

In *Lomera* (16 spp.) the venation is little reduced, CuP is not fused with 1A+2A in the fore wing, and the mid and hind tibiae each has a single apical spur. The epiphysis and basal segment of the fore tarsus are very long. The most specialised genera include *Clania* (9 spp.), *Hyalartea* (2 spp.) and *Elinostola* (4 spp.). The last two have lost the tibial spurs and one or more veins, and *Hyalartea* has also lost the epiphysis. *H. nigrescens* has almost transparent wings; the larva constructs a whitish silken case, tapering at each end, with prominent ribs, but without ornamentation (Fig. 41.33E). The food plant is *Eucalyptus*. The cylindrical larval case of *C. tenuis* (Fig. 41.26L) is ornamented with irregularly arranged lengths of twig from *Leptospermum* or other food plants (Fig. 41.33C).

**14. Eriocottidae** (Fig. 41.32A). Small to medium sized; head rough, with piliform scales, Australian species with pair of prominent raised neck tufts; ocelli present or absent (absent in Australian species); antennae filiform, pecten well developed, each flagellar segment with small group of lamellar scales on lateral surface, cilia long; with setose pilifers; proboscis present, naked; maxillary palps 4-segmented or reduced; labial palps 3-segmented, porrect, with long appressed scales and lateral bristles; epiphysis present (in Australian species) or absent; spurs 0-2-4; wings slender; fore wing (Fig. 41.27D) with chorda and M-stem present in cell,  $R_5$  to termen; valva long, with single ventral thorn-like sensillum; ovipositor telescopic, segment 8 with dorsal free or X-shaped costae. Pupa with single transverse row of teeth on abdominal terga.

This South American, African, European and Asian family (Nielsen 1978) has a single Australian representative, *Eucryptogona trichobathra* (Fig. 41.32A), known only from Broken Hill in western N.S.W. The adults fly in May (Nielsen and Robinson 1990).

**15. Tineidae** (Figs 41.32B–G). Small to medium sized; head (Fig. 41.28A) usually rough, with hair-scales, or smooth scaled; chaetosemata and ocelli absent; antennae simple filiform, scape usually with pecten; proboscis usually short, long in some genera; maxillary palps 5-segmented and folded, or reduced; labial palps drooping, porrect or ascending, 2nd segment usually with lateral bristles; epiphysis usually present, spurs 0-2-4, hind tibiae never smooth scaled; fore wing (Figs 41.27E, F) with chorda and M-stem often present in cell, M frequently



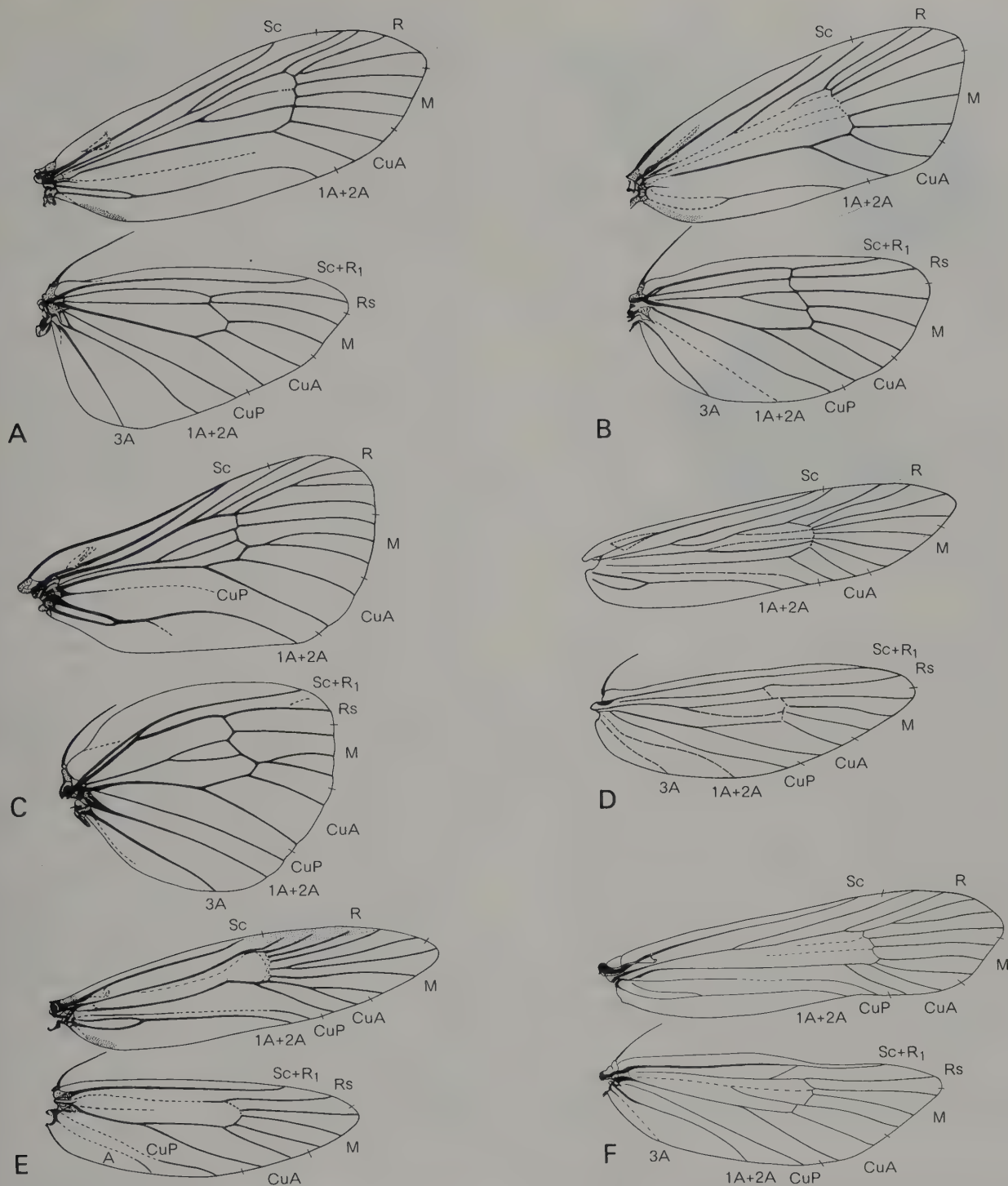


Fig. 41.27 Wing venation of Tineoidea: A, *Lepidoscia*, B, *Ardiosteres*, C, *Lomera*, Psychidae; D, *Eucryptogona*, Eriocottidae; E, *Monopis*, F, *Morophaga*, Tineidae. [A–C, E by B. Rankin; D by A. Hastings; F by I. F. B. Common]

forked,  $R_5$  to costa or apex; ovipositor usually telescopic. Eggs oval and slightly flattened. Larva sometimes case bearing, usually feeding on dried animal or vegetable matter, or on fungi, with 0–6 stemmata on each side of head, crochets in uniserial circle or ellipse. Pupa (Fig. 41.31c) usually with two transverse rows of spines on

terga, rarely with one; segments 4–7 movable in male, 4–6 in female; in larval shelter or cocoon.

The tineids are a heterogeneous group. Adults rest with the body flat, antennae bent backward and wings tent-like; when disturbed they often run rapidly rather than fly. The usually rough head, naked proboscis, bristly labial

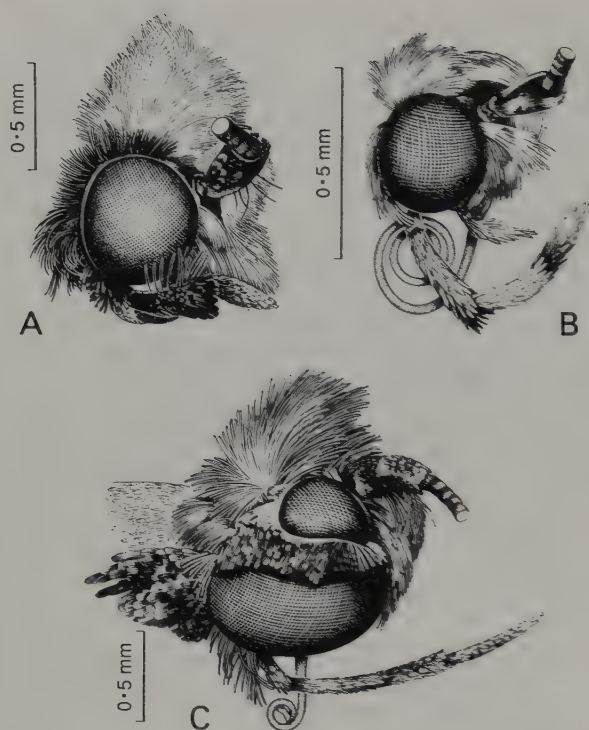


Fig. 41.28 Heads of Tineoidea: A, *Monopis*, Tineidae; B, *Acrocercops*, Gracillariidae; C, *Amphithera*, Roeslerstammiidae. [F. Nanninga]

palps, often long, folded maxillary palps, primitive venation, absence of pseudofrenular bristles and rough-scaled hind tibiae, are useful distinguishing characters. The family includes several cosmopolitan genera including pests of animal fibres and grain.

SCARDIINAE (fungus moths). Antennal pecten large; larva with 2 L setae on prothorax. *Tinissa* (2 spp.) from northern Qld has strongly developed apical and subapical scale tufts on the hind tibia. *Morphaga clonodes* is widespread in the south-western Pacific and eastern Australia, and the larvae have been reared from several species of bracket fungi (G. S. Robinson 1986).

NEMAPOGONINAE include a single endemic genus and the cosmopolitan *Nemapogon granella*, a pest of grain and foodstuffs.

TINEINAE. Second segment of labial palp with apical half-rosette of lateral bristles in addition to row of ventral bristles. *Tinea* (13 spp.) contains several cosmopolitan

pest species; among them the case-bearing clothes moths, *T. translucens* and *T. dubiella*, the commonest in Australia (G. S. Robinson 1979; Robinson and Nielsen 1987), and *T. columbariella* which feeds on natural keratin such as feathers in bird nests. Several native *Tinea* species, such as *T. corynephora* (Fig. 41.32B), occur mainly in Tas. and on the tablelands and mountains of the mainland; they have been reared from leaf litter. The cosmopolitan common clothes moth, *Tineola bisselliella*, is abundant in Australia and causes significant damage. *Niditinea fuscella* is another species common in bird nests and has been recorded from stored food products. *Acridotarsa* (Fig. 41.32D) (12 spp.) is known from Brazil and Africa and is widely distributed in mainland Australia; the long, slender larvae live in the nests of termites of the genera *Neotermes* and *Mastotermes*. In *Monopis* (Fig. 41.32C; 12 spp.) and related genera there is a small, semi-transparent area in the distal end of the cell of the fore wing (Fig. 41.35A). In some species, such as *M. chrysogramma*, the fertilised eggs are retained in the greatly enlarged vagina until just before hatching. The larvae are case bearing and feed on animal fibres.

MYRMECOZELINAE are well represented in Australia. *Setomorpha rutella* and *Lindera tessellatella*, sometimes placed in a separate subfamily, Setomorphinae, are cosmopolitan and feed on dry plant material and refuse. *Moerarchis* (Fig. 41.32E; 16 spp.) has been reared from dead stumps of grass-trees (*Xanthorrhoea*) and *Eucalyptus*, and from *Acacia* stems. Little is known about the biology of the narrow-winged genera *Timaea*, *Harmaclona*, *Mimoscopa* and *Gerontha*, but one species of *Mimoscopa* has been reared from larvae tying branchlets of *Casuarina*. *Edosa* (Fig. 41.32G; 40 spp.) is the second largest Australian tineid genus; many species have a purple and yellow fore wing pattern; although several species are common the biology remains unknown.

HIEROXESTINAE. Head smooth scaled, scales forming 'brow-ridge'; frons very oblique; scape long and slender; spurs long. Four genera occur in Australia. *Opogona* (28 spp.) includes small, brown, dark purple or yellow species; the larvae feed on dead plant material and several species are of economic importance. *O. omoscopa*, an Australian species which has become a pest overseas (D. R. Davis 1978), is known from plant potting material and is common indoors; *O. glycyphaga* injures sugar cane and bananas.

ERECHTHIINAE. Fore wing tips bent upwards in some

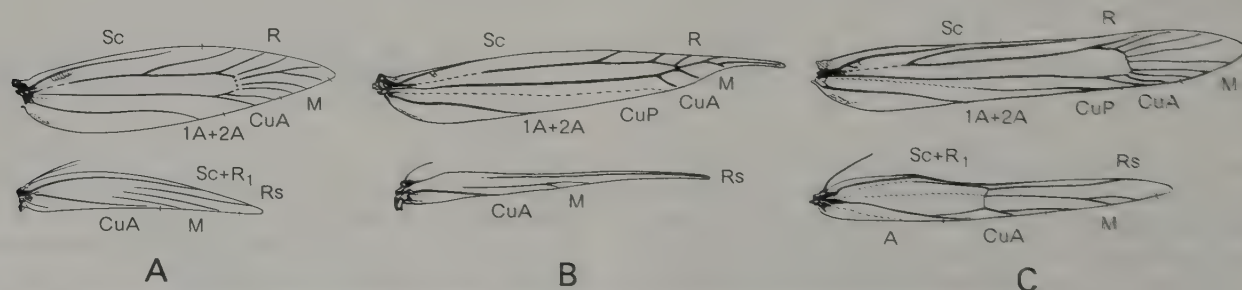


Fig. 41.29 Wing venation of Tineoidea: A, *Tinagma*, ♀, Douglasiidae; B, *Phyllocnistis*, Gracillariidae; C, *Macarostola*, Gracillariidae.

[A by J. Wedgbrow; B, C by B. Rankin]



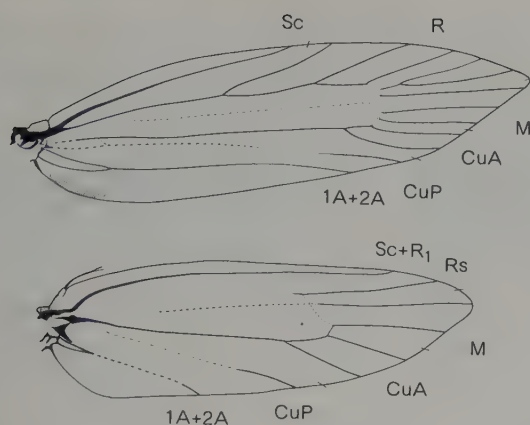


Fig. 41.30 Wing venation of *Thereutis*, Roeslerstammiidae.  
[I. F. B. Common]

species. Erechthiinae and Hieroxestinae have earlier been placed in the Lyonetiidae. The subfamily contains about 100 species in Australia. The largest genus, *Erechthias* (Fig. 41.32F; 67 spp.), is widely distributed outside Australia, and particularly diverse in the southern Pacific. The larvae feed on dead plant material and some species cause damage. One group of species has larvae boring in galls; those of the common *E. mystacinella* feed in galls on *Exocarpos* and *Acacia*, and in gall-like swellings of apples injured by woolly aphids.

**MEESSIINAE.** Very small. *Dryadaula* (9 spp.), with strongly asymmetrical male genitalia, has been reared from fungi. *Demobrotis* (5 spp.) is most likely associated with lichens. [G. S. Robinson and Nielsen in press]

**16. Roeslerstammiidae** (Amphitheridae) (Plate 7, F; Fig. 41.32H). Small, head (Fig. 41.28c) with raised hair scales on vertex, usually smooth scaled on frons; ocelli and chaetosemata absent; compound eyes sometimes with posterior indentation or divided horizontally by a scaled band; antennae usually longer than fore wing, with pecten; proboscis present, naked; maxillary palps reduced, 1-segmented; labial palps long, slender, curved, sensilla not in pit; epiphysis present; spurs 0-2-4, hind tibia with long piliform scales above and short, dense tuft on underside between spurs; fore wing (Fig. 41.30) with chorda and M-stem sometimes present in cell,  $R_4$  and  $R_5$  stalked or fused,  $R_5$  to costa;  $1A+2A$  with long fork; hind wing sometimes with pointed apex,  $M_3$  and  $CuA_1$  connate, stalked or fused; gnathos usually with 2 slender prongs; saccus usually present, bursa copulatrix usually with prominent signum. Larva with crochets in uniordinal lateral penellipse, sometimes partly biserial. Pupa with antennae reaching tip of abdomen or wrapped around abdomen, abdominal spiracles 7-8 sometimes slightly protruding, abdominal terga with transverse row of spines.

The larvae of *Thereutis* (6 spp.), *Macarangela* (Plate 7, F; 3 spp.) and *Nematobola* (3 spp.) first mine the leaves of their host plants; later instars feed fully exposed on the foliage; they pupate in a strong, white cocoon among leaf litter. The males of *Amphithera heteroleuca* (Fig. 41.32H) have large eyes divided horizontally. The greyish white

*Thereutis* have smaller, undivided eyes. *Chalcoteuches phlogera*, with metallic coppery green fore wings, recalls the Palearctic and Oriental type genus *Roeslerstammia*. [Kyrki 1983b; Moriuti 1978]

**17. Galacticidae** (Fig. 41.32I). Small; head smooth, with lamellar scales; ocelli and chaetosemata absent; antennae scaled, filiform or bipectinate, scape sometimes flattened, usually with pecten; proboscis usually long, unscaled; maxillary palps small, 2-segmented; labial palps porrect, apical segment very short; epiphysis present; spurs 0-2-4; fore wing with chorda and usually distinct M in cell, anterior branch of M vestigial,  $R_3$  to  $R_5$  approximate at base or  $R_2$  to  $R_4$  stalked,  $R_5$  to termen, CuP tubular distally,  $1A+2A$  with long fork; hind wing with M-stem present in cell, cross-veins very oblique, 2 anal veins,  $1A+2A$  broad at base; both male and female genitalia usually highly specialised. Larva with 3 L setae on one pinaculum fused to prothoracic shield; crochets biordinal in complete circle; at first in communal web, later enlarged web or singly between webbed leaves. Pupa with maxillary palps, abdomen with anterior transverse row of dorsal spines on segments 3-8 or 4-8, a posterior row on 3-7 or 4-6, and sometimes a posterior row of short setae encircling the posterior edge of segments 4-7, without cremaster; in fusiform, silk cocoon in larval web or in crevice.

The widespread genus *Homadaula* (Fig. 41.32I; 5 spp.) from S.A., W.A. and the N.T. belongs to this family. The greyish mottled adults remind one of species of *Prays* (Yponomeutidae). Larvae of *Homadaula myriospila* live in communal nests of webbed phyllodes of *Acacia ligulata* and pupate in a dense, white cocoon amongst dead phyllodes and faecal pellets in the middle of the webbed mass. [Clarke 1943; Kyrki 1990; Moriuti 1963]

**18. Bucculatricidae** (Fig. 41.36A). Very small; head with raised hair-scales on vertex, appressed lamellar scales on frons in Australian species; ocelli absent; chaetosemata absent in Australian species; antennae shorter than fore wing, with expanded scape and dense pecten forming eye-cap; proboscis short, unscaled; maxillary palps reduced, 1-segmented; labial palps very small, drooping, 3-segmented; epiphysis present, spurs 0-2-4, hind tibia with long hair-scales above and below between spurs; fore wing often with oblique striae along costa and dorsum, with 4 or 5 branches of R, 1 or 2 branches of M, CuA forming longitudinal axis,  $1A+2A$  without basal fork; hind wing without discal cell, Rs and M partly coalescent, Rs,  $M_1$  and  $M_2$  reaching margin; corpus bursae with signum of numerous spines or a dentate plate. Larva heteromorphic, with reduced number of crochets; in leaf-mine, leaf shelter, gall or bark-mine. Pupa with dorsal spines on T3-7, in dense, characteristically ribbed cocoon (Jäckh 1955).

*Bucculatrix* (9 spp.) occurs widely in Australia. *B. gossypii* attacks cotton in northern Australia; during the first 2 instars and part of the 3rd it is an apodous leaf-miner; it then spins an oval shelter on the leaf surface, in which it moults to the 4th instar. This older larva feeds exposed on the surface, skeletonising the leaf. It has normal thoracic legs, and ventral prolegs, each with 2

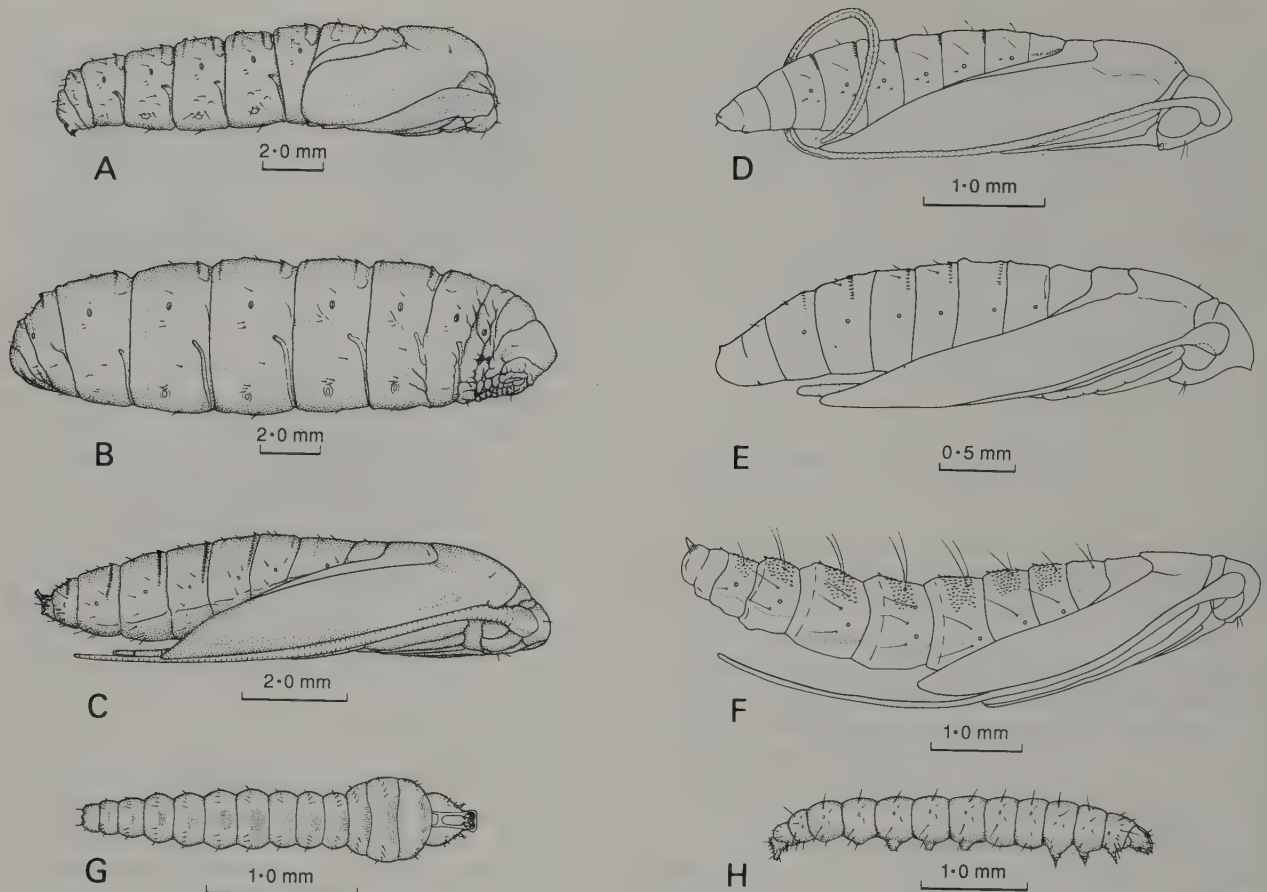


Fig. 41.31 Larvae and pupae of Tineoidea: A, B, pupa, ♂ and ♀, of *Lomera*, Psychidae; C, *Monopis*, pupa, Tineidae; D, *Thereutis*, pupa, Roeslerstammiidae; E, *Bucculatrix*, pupa, Bucculatricidae; F, *Caloptilia*, pupa, Gracillariidae; G, H, early and final instar larvae of *Acrocercops*, Gracillariidae. [A–C, G, H by B. Rankin; D–F by I. F. B. Common]

transverse bands of uniordinal crochets. Other Australian *Bucculatrix* feed on *Eucalyptus*, *Sterculia*, *Choretrum* and *Alphitonia*; all have a biology similar to that of *B. gossypii*, although the number of instars spent as a leaf-miner varies. *Ogmograptis*, with several species, may belong here. The larvae of *O. scribula* produce conspicuous, scribble-like mines (Fig. 41.34) in living bark of smooth-barked *Eucalyptus*, such as *E. pauciflora* and *E. micrantha*; the stiff, oval cocoon, from which the pupa is protruded at ecdysis, is very similar to that of *Bucculatrix*. No gall-forming species are known from Australia. [Scoble and Scholtz 1984]

**19. Douglassiidae** (Fig. 41.36B). Very small; head smooth scaled; ocelli prominent; chaetosemata absent; proboscis prominent; scape without pecten; maxillary palps rudimentary; labial palps short, drooping; hind tibiae with long hair-scales; fore wing (Fig. 41.29A) lanceolate, R with 4 or 5 branches to costa,  $R_5$  and  $M_1$  stalked, CuP weak or absent, female with subcostal retinaculum; hind wing lanceolate, frenulum in female of 1 or 2 bristles, Rs at or near long axis of wing, venation reduced, CuA free. Larva fusiform, prolegs small, crochets absent, with long setae, abdomen with L1 and L2 approximated; mining in leaves (*Klimeschia*), tunnelling in stems among flowers (*Tinagma*). Pupa in stem or leaf, with spines on

abdominal terga. Douglassiid host plants belong to the families Lamiaceae, Boraginaceae and Rosaceae.

*Tinagma leucanthes* (Fig. 41.36B) is a tiny black species with two transverse white bands on the fore wing, known from Sydney (N.S.W.) and Stradbroke I. (Qld). The prominent ocelli, unscaled proboscis, and the venation make recognition easy. Adults rest with the anterior part of the body raised. The larvae are unknown.

**20. Gracillariidae** (Plate 7, A; Figs 41.36C–E). Very small, slender; head (Fig. 41.28B) usually smooth scaled; ocelli and chaetosemata absent; antennae nearly as long as, or longer than, fore wing, filiform, scape slender, usually without pecten, sometimes with small eye-cap; proboscis present, unscaled; maxillary palps slender, porrect or ascending, 4-segmented, or reduced; labial palps slender, porrect or ascending; epiphysis present, spurs 0–2–4, hind tibiae smooth or with dorsal row of stiff bristles, never hairy, fore and mid tibiae sometimes thickened with scales; fore wing (Figs 41.29B, C) lanceolate or linear-lanceolate with long fringing piliform scales,  $R_5$  to costa or apex, some veins often lost,  $1A+2A$  without basal fork; hind wing lanceolate or linear, venation often reduced; male abdomen often with coremata on segments 7 and 8. Larva (Figs 41.31G, H) leaf- or gall-mining, at least in early stages, with heteromorphosis; early instars flattened,



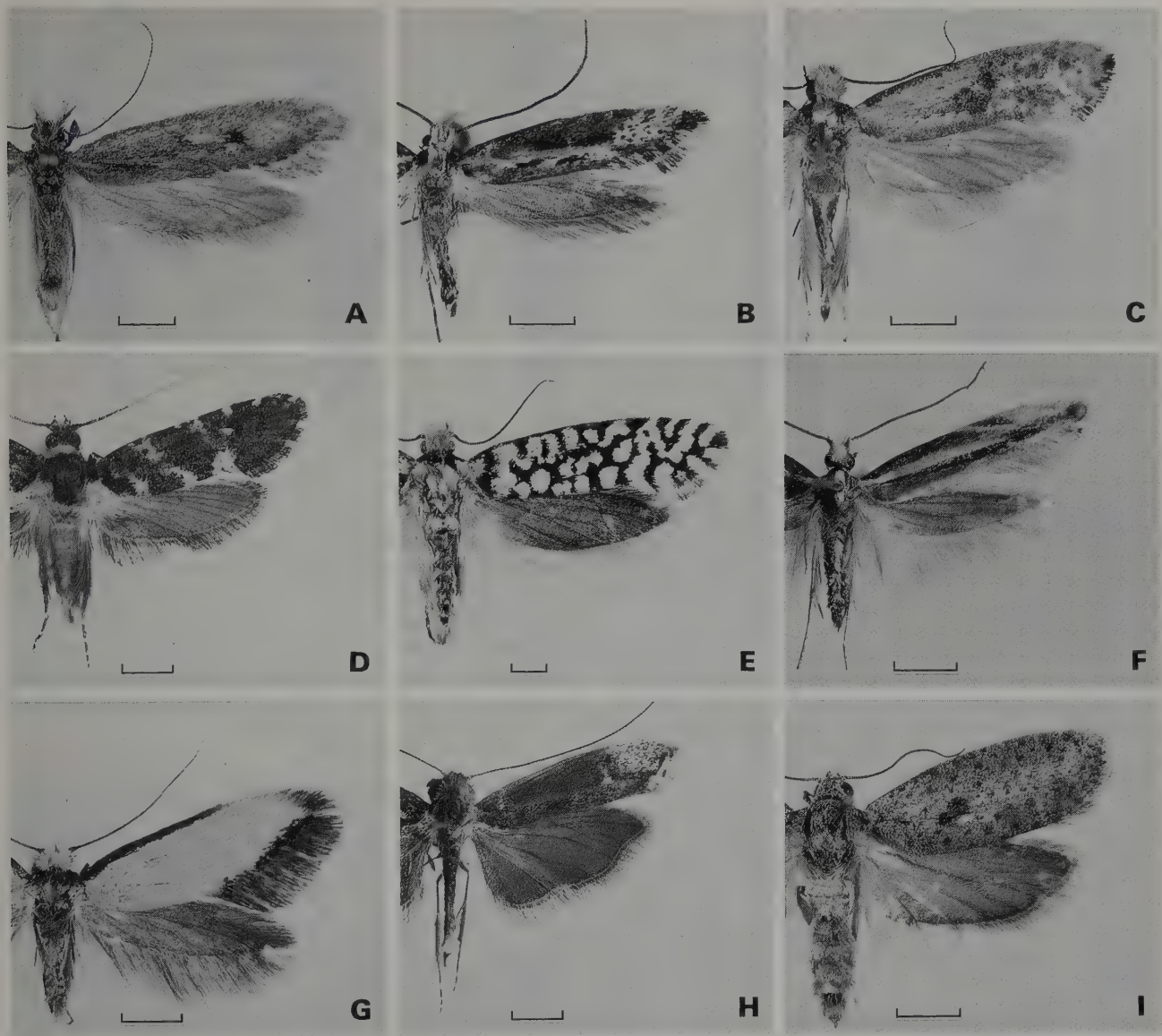


Fig. 41.32 A, *Eucryptogona trichobathra*, Eriocottidae; B, *Tinea corynephora*, C, *Monopis argillacea*, D, *Acridotarsa* sp., E, *Moerarchis clathrata*, F, *Erechthias acontistes*, G, *Edosa meliphanes*, Tineidae; H, *Amphithera heteroleuca*, Roeslerstammiidae; I, *Homadula myriospila*, Galactiidae. Scales = 2 mm. [J. Green, C. Lourandos]

with large blade-like mandibles, sap-feeding, thoracic legs and prolegs absent; after 2nd or 3rd ecdysis larvae of most Gracillariinae and Lithocolletinae feed on parenchyma, body cylindrical, thoracic legs present, prolegs on abdominal segments 3–5, crochets usually in lateral penellipse. Pupa (Fig. 41.31F) with antennae and proboscis often extending beyond wing tips; abdomen with fine scattered dorsal spines, segments 5–7 movable in male, 5–6 in female; usually in flattened cocoon.

GRACILLARIINAE are the largest subfamily in Australia and contain elegant, tiny moths, which usually rest with the anterior part of the body raised at a steep angle and the fore and mid legs prominently displayed (Fig. 41.35B). In *Caloptilia* (35 spp.) the larva is a leaf-miner at first, later cutting and rolling the edge of the leaf to form

a shelter within which the larva feeds and usually pupates. The introduced *C. azaleella* attacks azaleas in eastern Australia. The mature larvae of the endemic *Macarostola formosa* (Plate 7, A) abandons its rolled leaf shelter on *Acmena smithii* to pupate in an oval, flattened cocoon. In *Caloptilia* the fore and mid legs are ornamented with tufts of scales, but they are smooth in *Macarostola*. Most species in the composite genus *Acrocercops* (98 spp.) produce blister-like mines in leaves, pupating in an oval, flattened cocoon, either inside or outside the mine. The cocoon is usually ornamented with tiny, froth-like globules, the presence and number of which are of specific significance. The hind tibia of the adult has a series of stiff, dorsal bristles. *A. antimima* (Fig. 41.36D), on *Lomatia myricoides*, is one of several

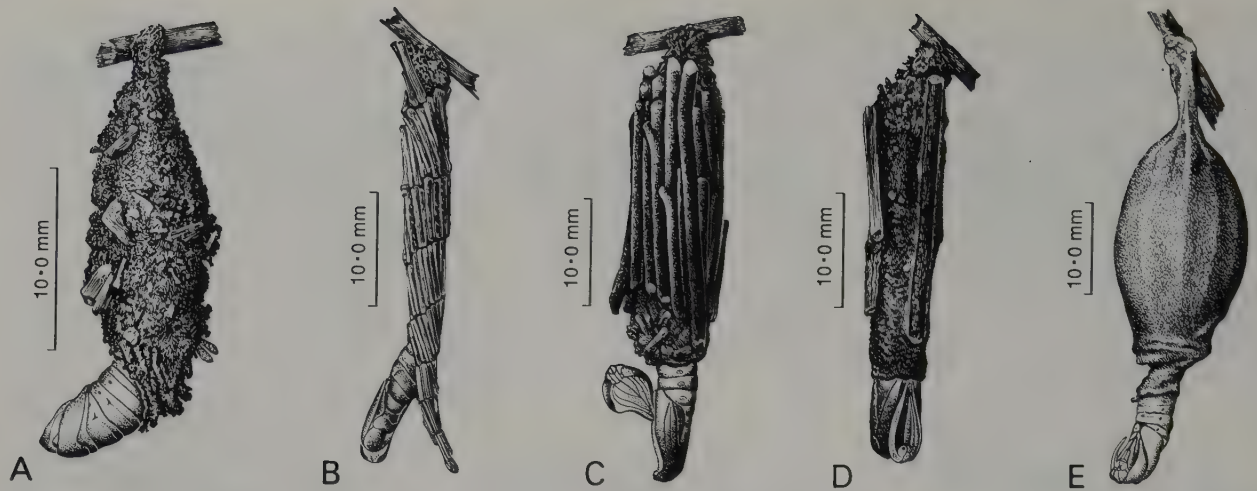


Fig. 41.33 Larval cases of Psychidae: A, *Cebysa*; B, *Lepidoscia*; C, *Clania*; D, *Trigonocyttara*; E, *Hyalarcta*.

[F. Nanninga]

similar species which attack Proteaceae. *A. plebeia* is a minor pest of *Acacia podalyriifolia*, and several species, such as *A. calicella* (Fig. 41.36E), mine the leaves of *Eucalyptus*. *A. tricuneatella* produces elongate mines in the leaves of the reed *Typha*.

LITHOCOLLETINAE are poorly represented in Australia; the adults rest with the bodies parallel to the surface. In Australia *Phyllonorycter* (11 spp.) contains tiny, orange and white species on Malvaceae, and black and white species on Fabaceae. The head is smooth scaled with a fringe of erect hair-scales above, and the maxillary palps are short. The larva forms a small mine in which the silk lining causes the epidermis to contract to form a characteristic cell. Several mines may occur in a single leaf. *P. aglaozona* mines in *Kennedia*, *Glycine* and sometimes in French beans and soy beans. The introduced *P. mesaniella* (Fig. 41.36C) is widely established in south-eastern Australia where it makes conspicuous mines on ornamental oaks (*Quercus*).

PHYLLOCNISTINAE comprise tiny, usually shining white species, with distinctive wing pattern, and with a prominent row of dorsal bristles on the hind tibiae. The scape forms a small eye-cap. The larva has a non-feeding, strongly modified, apodous last instar. The larvae produce silvery, serpentine mines in the epidermis of leaves, superficially suggesting the trails of snails. Pupation occurs in a silk-lined chamber formed at the end of the mine by partially folding in the sides. All the known species belong to the genus *Phyllocnistis* (14 spp.). *P. diaugella* is common in coastal eastern Australia, often covering the upper surface of the leaves of *Breynia oblongifolia* and *Phyllanthus* with its mines. The widely distributed *P. citrella* produces tortuous, linear mines on both sides of the young leaves of *Citrus*, causing them to become badly distorted. [Vári 1961; Kumata 1982]

#### Superfamily YPONOMEUTOIDEA

Very small to medium sized, ocelli present or absent; chaetosemata usually absent; scape sometimes with pecten; proboscis naked; maxillary palps small, 1-4-

segmented; labial palps short, drooping or moderately ascending; epiphysis present; spurs 0-2-4, rarely 0-2-0; fore wing with M rarely retained in discal cell, chorda and pterostigma often present,  $R_5$  usually to termen, venation sometimes reduced; retinaculum in female sometimes a subcostal scale-tuft; hind tibiae usually smooth, abdomen sometimes with inconspicuous dorsal spining, S2 of tineid type and usually with transverse rim near anterior

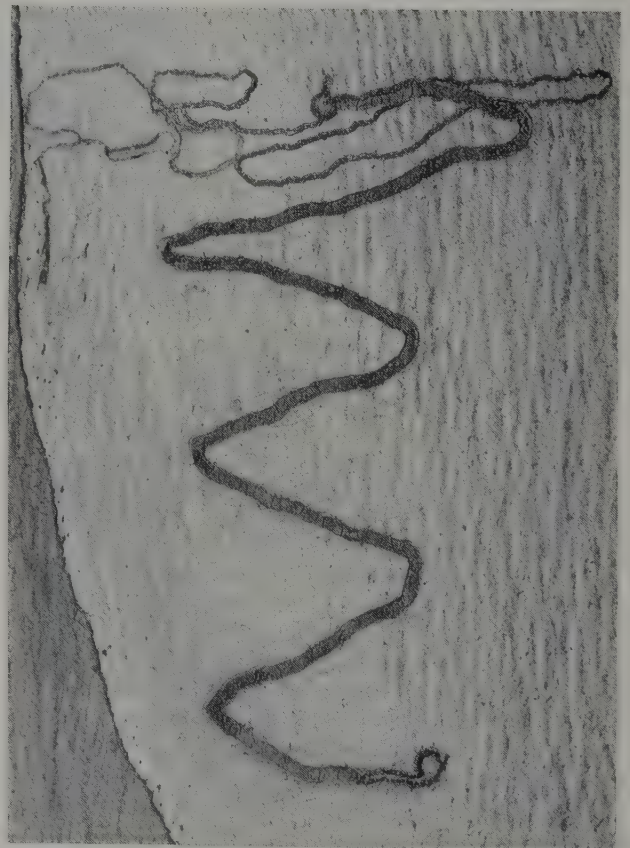


Fig. 41.34 The 'scribble' mine of the scribble moth, *Ogmograptis*, Bucculatricidae; overall height of scribble 11 cm.

[M. S. Upton]



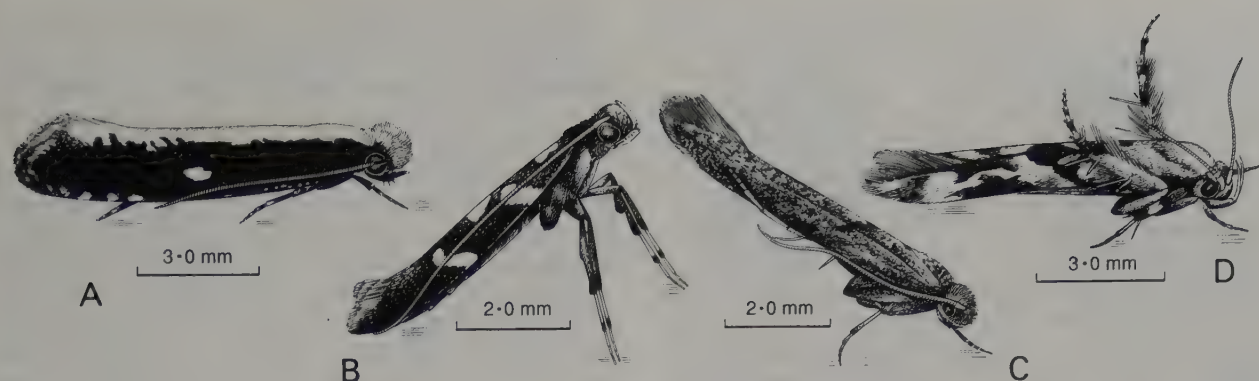


Fig. 41.35 Adults, resting: A, *Monopis*, Tineidae; B, *Caloptilia*, Gracillariidae; C, *Zelleria*, Yponomeutidae; D, *Stathmopoda*, Oecophoridae. [F. Nanninga]

margin, male segment 8 with pleural lobes present and often with paired coremata. Larva with 3 prespiracular (L) setae on prothorax (only 2 in Glyphipterigidae), crochets in a uniordinal, uniserial to multiserial circle, occasionally in transverse band or absent; boring in stems, mining in leaves, feeding beneath a slight webbing, or in a more extensive webbing. Pupa without dorsal abdominal spines, or rarely with dorsal transverse ridges (one non-Australian group); in larval gallery or in fusiform or oval, silken, sometimes network cocoon or exposed, usually not protruded from cocoon or shelter at ecdysis.

The overall primitive nature of this superfamily is demonstrated by the tineid type S2 of the adults. The phylogeny of the three ditrysian superfamilies with this type of sternum (Kyrki 1983a), Tineoidea, Yponomeutoidea and Gelechioidea, is not resolved. The Yponomeutoidea has been defined (Kyrki 1984, 1990) and many previously included groups have been removed (see Kyrki 1984 for review). Groups removed include Epermeniidae, Bucculatricidae, Douglassiidae, Roeslerstammiidae, *Homadula*, *Lactura* and associated genera, Sesiidae, Choreutidae, Immidae and Brachodidae. [Moriuti 1977]

#### Key to the Families of Yponomeutoidea Known in Australia

1. Ocelli present ..... 2  
Ocelli absent ..... 4
- 2(1). Fore wings with shining metallic coloration or labial palps with transverse pattern of light and dark bars and fore wing often with distinct white marks ..... 3  
Fore wings without metallic coloration and labial palps without distinct transverse light and dark bars ..... **Plutellidae** (p. 857)
- 3(2). Labial palps with light and dark bars; fore wing with pterostigma, hind wing cell closed ..... **Glyphipterigidae** (p. 857)  
Labial palps with distinct pattern, fore wing without pterostigma; hind wing cell open ..... **Heliodinidae** (p. 857)
- 4(1). Head with raised, piliform scales between antennae ..... **Lyonetiidae** (p. 857)  
Head with appressed or roughened lamellar scales ..... 5
- 5(4). Abdominal segment 8 in ♂ with sclerotised Y- or V-shaped sternum; ♀ with long apophyses .... **Argyresthiidae** (p. 856)  
Abdominal segment 8 in ♂ without Y- or V-shaped sternum; ♀ apophyses not unusually long ..... **Yponomeutidae** (p. 855)

**21. Yponomeutidae** (Plate 7, F; Fig. 41.36F). Small to very small, head (Fig. 41.37A) with smooth or roughened lamellar scales, ocelli absent; chaetosemata present or absent; antennae with or without pecten, proboscis usually present, naked; maxillary palps small, 1–4-segmented; labial palps smooth scaled and often up-turned; epiphys present; spurs 0–2–4 or 0–2–0; fore wing (Fig. 41.38A) usually with pterostigma, male retinaculum near base of Sc, wing venation little reduced, chorda and M-stem present in cell, Rs to termen,  $R_4$  and  $R_5$  stalked or separate, CuP present at margin, 1A+2A forked; abdominal terga sometimes spined, male segment 8 with large pleural lobes, valva usually broadly rounded. Larva with distinct pinacula, pinacula SD1 and SD2 on meso- and metathorax fused, L1 and L2 widely separate on thorax and abdominal segments 1–8, ventral prolegs with complete circles of tri- to multiserial crochets; larva lives singly in

slight webbing on leaves or gregariously in extensive webs, pupation in fusiform cocoon in larval web or near-by. Pupa (Fig. 41.39A) sometimes with cremaster and terminal hooked spines; not protruded from cocoon at ecdysis. Adults rest with antennae turned back and appressed; some groups rest with the body raised obliquely and head depressed (Fig. 41.35C).

YPONOMEUTINAE, with spined terga and S8 more sclerotised than S7, are well represented in Australia. *Yponomeuta* (6 spp.) has white fore wings with numerous black spots; the larvae live communally in often large webs. *Y. paurodes* (Fig. 41.36F) and other *Yponomeuta* species occur in eastern Australia, often in rainforest. *Zelleria* (20 spp.) occurs mainly in southern Australia; all have long and narrow wings (Fig. 41.35C).

ATTEVINAE, without pecten and with chaetosemata, contain brightly coloured species in *Atteva* (6 spp.). A.

*niphocosma* (Plate 7, L) occurs in eastern Australia and has gregarious larvae feeding on the rainforest tree *Polyscias murrayi*.

PRAYDINAE, with a pecten and a discrete sacculus in the male genitalia, are represented in Australia by *Prays* (7 spp.). The larvae feed within a slight shelter of webbing on flowers, buds and leaves of Rutaceae. Two species, *P. nephelomima* and *P. parilis*, cause damage to *Citrus* flowers in eastern Australia.

**22. Argyresthiidae** (Fig. 41.36G). Very small; head with roughened lamellar scales on vertex and appressed lamellar scales on frons; ocelli and chaetosemata absent; antennae with pecten, filiform; proboscis present; maxillary palps 1-segmented; labial palps rather long, slightly

curved; epiphysis present; spurs 0-2-4; fore wing (Fig. 41.38B) with pterostigma,  $R_4$  and  $R_5$  stalked or separate, chorda and M-stem vestigial, CuP present at margin, 1A +2A with short fork; hind wing with  $M_1+M_2$  long stalked; abdomen without dorsal spines; male segment 8 with Y- or V-shaped thickening on sternum, large pleural lobes and pair of coremata; socii of male genitalia with characteristic scales; signum usually bilobed. Larva endophagous, thorax and abdomen densely spinulose, thoracic legs short, crochets on ventral prolegs in uniordinal, uniserial circle or transverse band. L1 and L2 approximate on abdominal segments 1-8; larvae bore in buds, fruits and twigs; pupation in cocoon, often in larval gallery. Pupa without cremaster, but with apical hooked setae.



Fig. 41.36 A, *Bucculatrix* sp., Bucculatricidae; B, *Tinagma leucanthes*, Douglasiidae; C, *Phyllonorycter messaniella*, D, *Acrocercops anemima*, E, *A. callicella*, Gracillariidae; F, *Yponomeuta paurodes*, Yponomeutidae; G, *Argyresthia notaleuca*, Argyresthiidae; H, *Leuroperma sera*, Plutellidae; I, *Glyphipterix gemmipunctella*, Glyphipterigidae. Scales: A-C, G = 1 mm; D-F, H, I = 2 mm.

[J. Green, C. Lourandos, E. Slater]



The family is represented in Australia by *Argyresthia notoleuca* (Fig. 41.36G), which occurs in rainforest in northern Qld. Adults rest with the head depressed and the body raised at a steep angle.

**23. Plutellidae** (Fig. 41.36H). Small; head with smooth or roughened lamellar scales on vertex, appressed lamellar scales on frons; ocelli present; chaetosemata absent; antennae with pecten, filiform; proboscis present; maxillary palps 4-segmented, porrect; labial palps porrect or ascending, often with projecting tuft on 2nd segment; epiphysis present; spurs 0-2-4; fore wing (Fig. 41.38C) with pterostigma to  $R_2$ ,  $R_4$  and  $R_5$  separate,  $CuA_1$  and  $CuA_2$  separate, connate or stalked; hind wing as broad as or broader than fore wing; abdomen without dorsal spines, segment 8 in male with pair of coremata; tegumen reduced; female lamella postvaginalis reduced to 2 small setose lobes. Larval body densely spinulose, pinacula distinct, L1 and L2 approximate on meso- and metathorax, widely separate on abdominal segments 1-8; crochets uniserial, in complete or broken circle, sometimes partly biserial; in slight web on leaves, pupation in open-mesh cocoon. Pupa (Fig. 41.39B) with segment 10 bearing more than 16 hooked setae. The cosmopolitan pest-species *Plutella xylostella* (Griggs 1986) skeletonises the foliage of Brassicaceae, both cultivated and native. *Leuoperna sera* (Fig. 41.36H), widely distributed in the Old World, also feeds on Brassicaceae.

**24. Glyphipterigidae** (Fig. 41.36I). Very small to small; head (Fig. 41.37B) with smooth lamellar scales; ocelli prominent; chaetosemata absent; antennae without pecten, filiform; proboscis present; maxillary palps small, 1- to 4-segmented; labial palps usually curved, 2nd segment thickened, usually with transverse pattern of light and dark bars; epiphysis present; spurs 0-2-4; fore wing (Fig. 41.38D) with pterostigma to  $R_2$ , chorda present, M-stem vestigial,  $R_4$  and  $R_5$  usually separate, rarely stalked,  $CuP$  present at margin or vestigial; hind wing with  $M_2$  arising closer to  $M_1$  than  $M_3$ ; abdomen of male with pleural lobes of 8 fused with tergum, segment 8 often with coremata; tegumen reduced, gnathos absent, anal tube long. Larval cuticle spinulose, prothoracic L group bisetose, spiracle on segment 8 enlarged and set postero-dorsally, abdominal segments 8 and 9 sometimes with dorsal sclerotised shields, prolegs with crochets few, in lateral penellipse or transverse band, or absent; borers in buds, stems and seeds of monocotyledons, pupation away from host in flimsy cocoon. Pupa with small projection on head, prothoracic spiracles protruding, abdomen without dorsal spines, segment 10 with up to 12 hooked setae, not protruded at eclosion.

By far the largest Australian genus is *Glyphipterix* (60 spp.) in which the fore wings have brilliant metallic markings. The moths fly during the day in damp places. The adults often feed at flowers or rest on their host plants, species of Juncaceae, Cyperaceae and Poaceae, and have the habit of rhythmically raising and lowering their wings. The majority of the species occur in Tas. and south-eastern mainland Australia. *G. gemmipunctella* (Fig. 41.36I), which occurs from the Atherton Tableland (Qld) to Vic., has the basal half of the hind wing bright

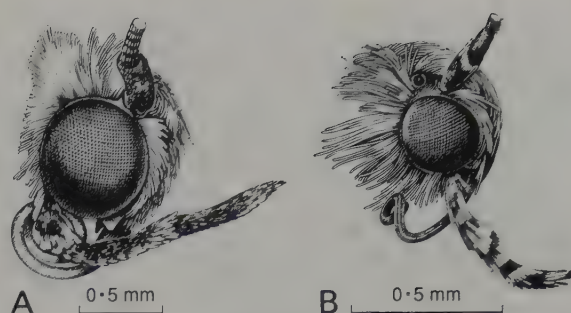


Fig. 41.37 Heads of Yponomeutoidea: A, *Yponomeuta*, Yponomeutidae; B, *Glyphipterix*, Glyphipterigidae. [F. Nanninga]

yellow and is attracted to light. [Arita 1987; Diakonoff 1986; Heppner 1982; Kyrki and Itämes 1986]

**25. Heliodinidae** (Plate 7, C; Fig. 41.40A). Very small; head smooth scaled, shining metallic; ocelli present, prominent; chaetosemata absent; antenna almost as long as fore wing, pecten absent, flagellum filiform, thickened in male; proboscis present; maxillary palps 2-segmented, very small; labial palps short, curved or drooping; epiphysis present; spurs 0-2-4; fore wing (Fig. 41.38E) with brilliant metallic markings, without pterostigma, one vein, probably  $M_3$ , absent,  $CuP$  reduced or absent, fork of  $1A+2A$  small; hind wing with a single frenular bristle in female, discal cell not closed by cross-vein  $M-CuA$ ,  $CuP$  absent; abdomen without dorsal spines; aedeagus and saccus extremely long and slender; corpus bursae with close-set star-shaped spicules. Larval prothorax with three L setae, abdominal segments 1-7 with L1 and L2 on separate pinacula and widely separate on 8; crochets in unior-dinal circle; leaf-mining or in web among fruits, pupation on host plant. Pupa without distinct maxillary palps, abdominal segments not movable, and without dorsal spines, with strong lateral ridges and strong lateral and dorsal bristles.

The Heliodinidae are represented in Australia by only four species in two genera. *Heliodines princeps* (Plate 7, C) is known from two Qld specimens. *Epicroesa* (Fig. 41.40A; 3 spp.) which also occurs in New Guinea and Japan, is restricted to Qld. The early stages are unknown, but the adults are most likely day flying. [Kyrki 1984; Diakonoff and Arita 1979]

**26. Lyonetiidae** (Fig. 41.40B). Very small; head smooth scaled with scale-tuft between antennae; ocelli and chaetosemata absent; antennae two-thirds of fore wing, scape with eye-cap; proboscis short; maxillary palps minute, 1-segmented; labial palps short, porrect or drooping; epiphysis present; spurs 0-2-4; hind tibiae with long piliform scales on upper surface; fore wing (Fig. 41.38F) narrow lanceolate, without pterostigma, venation markedly reduced, all R to costa,  $CuP$  absent and sometimes  $1A+2A$  without basal fork; hind wing with 2 fine frenular bristles in female, with fringing scales several times width of wing, cell not closed and rarely more than 5 veins; abdomen with spined terga in Cemiostominae, coremata often present on 8 and T8 often modified; ovipositor piercing in Lyonetiinae. Larva leaf-mining,

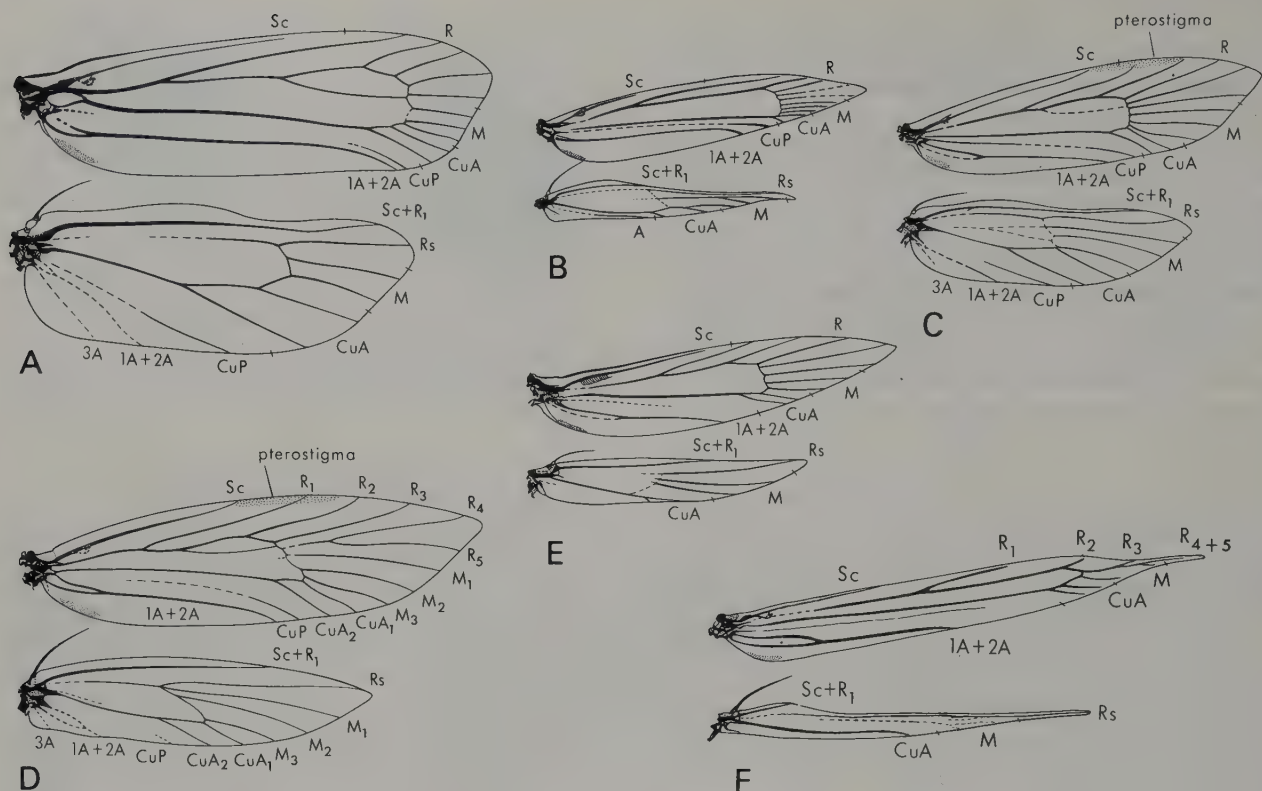


Fig. 41.38 Wing venation of Yponomeutoidea: A, *Yponomeuta*, Yponomeutidae; B, *Argyresthia*, Argyresthiidae; C, *Plutella*, Plutellidae; D, *Glyphipterix*, Glyphipterigidae; E, *Heliodines*, *Heliodinidae*; F, *Stegommata*, Lyonetiidae. [A–E by J. Wedgbrow; F by B. Rankin]

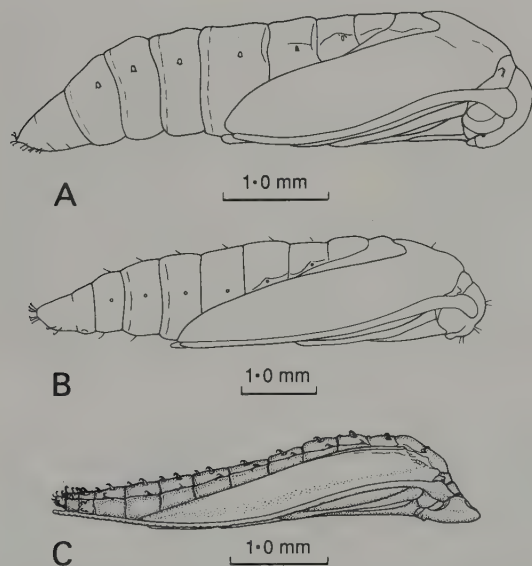


Fig. 41.39 Pupae of Yponomeutoidea: A, *Prays*, Yponomeutidae; B, *Plutella*, Plutellidae; C, *Stegommata*, Lyonetiidae. [A, B by I. F. B. Common; C by B. Rankin]

flattened, early instars usually without prolegs, late instars with crochets in uniordinal circle; prothorax with 3 L setae, L2 absent on abdominal segments 1–8 in some groups, when present L1 and L2 widely separate on abdominal segments. Pupa (Fig. 41.39C) long and slender

to short and broad, maxillary palps small or absent, abdomen without movement of any segments; pupation in cocoon or suspended on host by a few strands of silk.

CEMIOSTOMINAE (Leucopterinae) are tiny moths with an eye-cap, shining white fore wings, a metallic spot and specialised scales near the tornus, and spined abdominal terga. Typically, larvae of *Leucoptera* (Fig. 41.40B; 18 spp.) first make a linear mine in a leaf which then broadens into a blotch; when mature the larva leaves the mine and pupates in a white cocoon externally on a leaf or the stem of the host; the larval skin is deposited outside the cocoon (Deschka 1985). *L. daricella*, which occurs in Africa, Asia and northern Qld, mines in *Plumbago*. Other species mine in *Alphitonia* and *Canthium*. [Bradley and Carter 1982]

BEDELLIINAE have a dense pecten,  $R_3$ ,  $R_4$ ,  $R_5$  and  $M_{1+2}$  on a common stalk from the pointed apex of the cell, grey fore wings sprinkled with darker scales, and pupae with a conical projection. *Bedellia* (22 spp.) is nearly cosmopolitan. *B. somnulentella* is a pest of sweet potato, *Ipomoea batatas*; the larva first makes a short linear leaf-mine which it leaves to make a blotch mine; it pupates exposed outside the mine among a few silk strands on the underside of a leaf. Another Australian species feeds in a similar way on *Parsonsia*. [Kuroko 1972]

LYONETIINAE are often recognised by their delicate fore wing pattern. They have an eye-cap, very narrow wings, extremely short abdominal terga and piercing ovipositor. The parenchyma-feeding larvae excavate blotch mines in



leaves, sometimes with an initial linear mine. When mature the larva pupates in a flimsy elliptical cocoon suspended hammock-wise from silk strands stretched across a hollow, often near the edge of a leaf. *Stegommata sulfuratella* is white, with larvae producing blotch mines in young leaves of *Banksia integrifolia*; *S. leptomitella* is a locally common leaf-miner on *Hakea saligna*.

### Superfamily GELECHIOIDEA

Ocelli present or absent; chaetosemata absent; scape often with pecten; proboscis with dense, imbricated scales towards base, rarely reduced; maxillary palps small, mostly 4-segmented, folded over base of proboscis, rarely reduced; labial palps usually recurved, apical segment often exceeding vertex, usually tapering, acute; epiphysis usually present; spurs 0-2-4; fore wing with M rarely present in discal cell, chorda vestigial or absent, retinaculum in female often subcubital; hind wing with venation sometimes reduced, CuA rarely with basal pecten of hairs, CuP often absent, female frenulum usually with 3 bristles; S2 of tineid type; abdomen often with prominent dorsal spines. Larva with 3 L setae on prothorax, crochets in a circle, penellipse, or rarely in 2 transverse rows, abdominal setae L1 and L2 approximated; concealed

feeders, case-bearing, tunnelling in stems or fruits, gall-forming, leaf-mining, joining foliage, or feeding beneath silken shelter. Pupa usually with labial palps and fore femora concealed, without dorsal abdominal spines, usually segments 5-7 movable in male, 5-6 in female; usually in larval shelter, not protruded from shelter or cocoon at ecdysis.

Most gelechioids can be easily recognised by the densely scaled proboscis, the base of which is clasped by the small, 4-segmented maxillary palps. In the Coleophoridae, Agonoxenidae, Elachistidae and a few Oecophoridae, the maxillary palps are reduced. Genera usually referred to the families Xyloryctidae, and those related to *Stathmopoda* and to *Agriophara* are here treated as subfamilies Xyloryctinae, Stathmopodinae and Stenomatinae of the Oecophoridae (Hodges 1978).

With 17 families this is by far the largest superfamily, but the families Blastodacnidae, Momphidae, Symmocidae and Holcopogonidae have not been recorded from Australia. More than half of the species are Oecophoridae. The Gelechiidae and Cosmopterigidae are also large families containing many endemic genera. At the other extreme are the small families Coleophoridae and Agonoxenidae.

### Key to the Families of Gelechioidea Known in Australia

1. Hind wing narrow, lanceolate, linear-lanceolate or linear, narrower than its fringe ..... 2  
Hind wing ovate-lanceolate, ovate or trapezoidal with sinuate or emarginate termen usually wider or as wide as its fringe ..... 10
- 2(1). Fore wing with  $R_2$  approximated at base to upper angle of discal cell, remote from  $R_1$  ..... 3  
Fore wing with  $R_2$  well before upper angle of discal cell ..... 4
- 3(2). Fore wing with strong pterostigma; ♀ with both subcubital and radial retinacula ..... **Blastobasidae** (p. 867)  
Fore wing without pterostigma; ♀ with only subcubital retinaculum ..... **Oecophoridae-STATHMOPODINAE** (p. 860)
- 4(2). Fore wing with  $R_5$  to termen; a series of long setae near inner margin beneath; hind wing with similar subcostal series above ..... **Scythrididae** (p. 869)  
Fore wing with  $R_5$  to costa; without long setae beneath fore wing and above hind wing ..... 5
- 5(4). Gnathos in ♂ terminating in one or two spined knobs ..... 6  
Gnathos in ♂ not spinose or gnathos absent ..... 8
- 6(5). Abdominal terga each bearing 2 small, longitudinal patches of short spines, not covered by scales ..... **Coleophoridae** (p. 864)  
Abdominal terga without spines ..... 7
- 7(6). Frons strongly oblique; labial palps flattened; antennae porrect in repose ..... **Agonoxenidae** (p. 865)  
Frons vertical; labial palps not flattened; antennae turned back in repose ..... **Elachistidae** (p. 865)
- 8(5). Abdominal terga each bearing 2 longitudinal patches of spines, partially or wholly obscured by scales ..... **Batrachedridae** (p. 864)  
Abdominal terga with spines more generally distributed or spines absent ..... 9
- 9(8). Abdominal terga with spines generally distributed; genitalia of ♂ symmetrical, uncus and gnathos present, gnathos arms fused medially ..... **Oecophoridae-OECOPHORINAE** (pt, p. 860)  
Abdominal terga without spines; genitalia of ♂ usually asymmetrical, either uncus or gnathos absent, gnathos arms not fused medially, usually asymmetrical ..... **Cosmopterigidae** (p. 868)
- 10(1). CuP absent as a tubular vein from both wings; hind wing often with emarginate termen; ♀ with radial retinaculum of specialised scales ..... **Gelechiidae** (p. 868)  
CuP present as a tubular vein at least in hind wing; termen of hind wing not emarginate; ♀ with subcubital retinaculum of erect scales ..... 11
- 11(10). Hind wing with  $R_s$  and  $M_1$  well separated at base, parallel or slightly divergent ..... 12  
Hind wing with  $R_s$  and  $M_1$  closely approximated at base, connate or stalked, divergent ..... 15
- 12(11). Gnathos in ♂ with 1, 2 or 4 spinose knobs ..... **Depressariidae** (pt, p. 864)  
Gnathos in ♂ not spinose ..... 13
- 13(12). Sacculus of ♂ valva with discrete, triangular sclerite ..... **Hypertrophidae** (p. 864)  
Sacculus of ♂ valva without discrete, triangular sclerite ..... 14
- 14(13). Hind wing with  $M_2$  usually not arising nearer to  $M_1$  than to  $M_3$ ; if  $M_2$  nearer to  $M_1$  or equidistant from  $M_1$  and  $M_3$ ,

- then abdomen with dorsal spines ..... **Oecophoridae-OECOPHORINAE** (pt, p. 860)
- Hind wing with  $M_2$  arising nearer to  $M_1$  than to  $M_3$ , or rarely equidistant from  $M_1$  and  $M_3$ ; abdomen without dorsal spines ..... **Ethmiidae** (p. 867)
- 15(11). Hind wing with  $Sc+R_1$  approaching  $Rs$  near or before end of cell ..... **Oecophoridae-STENOMATINAE** (p. 860)
- Hind wing with  $Sc+R_1$  diverging from  $Rs$  well before end of cell ..... 16
- 16(15). Fore wing with a series of long setae near inner margin beneath; hind wing with similar subcostal series above; antennae porrect in repose ..... **Lecithoceridae** (p. 869)
- Fore wing and hind wing without such series of long setae; antennae turned back in repose ..... 17
- 17(16). Gnathos in ♂ with 1, 2 or 4 spinose knobs; abdomen usually without dorsal spines ..... **Depressariidae** (pt, p. 864)
- Gnathos in ♂ not spinose; abdomen usually with dorsal spines ..... **Oecophoridae-XYLORYCTINAE, AUTOSTICHINAE** (p. 860)

**27. Oecophoridae** (Plates 6, F, ZD; 7, B, E, H; Figs 41.40C–J). Very small to medium sized; head (Figs 41.41A–D) usually smooth scaled; ocelli rarely present; antennae simple, ciliate or pectinate, scape often with pecten in Oecophorinae; proboscis rarely short or vestigial; maxillary palps 3- or 4-segmented, folded over base of proboscis (Fig. 41.41A) or rarely reduced to 2 segments; labial palps recurved, often exceeding vertex, apical segment usually slender, tapering, acute; epiphysis present, hind tibiae with long piliform scales; fore wing (Figs 41.42A–D) varying from lanceolate to broad, without pterostigma,  $R_4$  and  $R_5$  usually stalked, never more than one vein lost, CuP present at least towards margin; hind wing with  $Sc$  and  $Rs$  usually well separated,  $R_1$  often present, sometimes (Stenomatinae)  $Sc+R_1$  approaches cell towards upper angle.  $Rs$  and  $M_1$  well separated at base, parallel or slightly divergent (Oecophorinae), connate or stalked (Stathmopodinae, Autostichinae, Xyloryctinae, Stenomatinae),  $M_2$  usually arising nearer to  $M_3$  than to  $M_1$ , CuP present in outer half; female sometimes brachypterous; frenulum in female with 3, rarely 2, bristles;  $S_2$  with reduced apodemes and distinct rods, abdomen often with dorsal spines; male genitalia various, gnathos never with a spinose knob. Larva with crochets in uniordinal or biordinal circle, ellipse or penellipse, rarely triordinal; tunnelling in wood, stems, branches or in flowers or galls, joining leaves, among detritus, or in tunnels in soil; some form portable cases and a few are leaf-miners. Pupa (Figs 41.45A, B) usually with large maxillary palps, abdominal segments 5–7 in male, 5–6 in female movable; in larval shelter.

The family has reached a remarkable degree of development in Australia, especially in the Oecophorinae and Xyloryctinae. In most Australian species of OECOPHORINAE  $Rs$  and  $M_1$  of the hind wing are nearly parallel (Fig. 41.42A), the abdominal terga are densely spinose, and the male usually has a beak-like gnathos. The larval habits are diverse, but many feed on dead *Eucalyptus* leaves on the forest floor. Some species of *Garrha* (53 spp.) cut oval, flattened cases from fallen leaves; other genera, such as *Thema* (20 spp.), join dead leaves on the ground or in tree crevices. *G. carnea* and *T. chlorochyta* (Fig. 41.40C) are good examples. Living *Eucalyptus* leaves provide food for many species, some of which construct portable cases, and others spin shelters between adjacent leaves or live in tubular shelters among

the twigs. *Chrysonoma fascialis* forms a flat case of two fragments of leaf, usually on juvenile foliage near the ground. A short length of hollowed-out twig is used as a portable case (Fig. 41.46B) by *Hippomacha callista* (Fig. 41.40D), the open end being blocked by the modified head capsule of the larva. In *Aristeis hepialella* the case resembles a snail shell, made from a series of successively larger, spirally arranged, overlapping fragments of eucalypt leaf (Fig. 41.46C). Some species, such as *Heliocausta hemiteles*, live gregariously in silken tubes spun in a bunch of tied leaves. *Wingia rectiorella* (Plate 7, B) spins a solitary silken shelter on *Leptospermum*.

Few native Oecophorinae are known pests, but *Philobota productella* (Fig. 41.40E) and related species damage grass pastures in the south-east. Larvae form short vertical tunnels in soil, emerging to feed on grass. *Barea consignatella* and related species sometimes damage sapwood in damp structural timbers; in Tas. *Barea* species often are important decomposers of litter in temperate rainforest. Introduced stored-product pests include *Hofmannophila pseudospretella* and *Endrosis sarcitrella*.

STATHMOPODINAE adults are usually very small, with smooth-scaled head (Fig. 41.41C) and very narrow wings (Fig. 41.42B). The hind tibiae and tarsi usually have whorls of stiff bristles. Many rest with the hind legs raised (Fig. 41.35D). *Snellenia* (4 spp.) and *Pseudaegeria* (4 spp.) contain handsome diurnal species which visit flowers. *S. lineata* (Plates 6, F; 7, E) has thickened antennae and enormous labial palps; it bears a close resemblance to *Metriorrhynchus* (COLE) which feed at the same flowers. *Coracistis erythrocosma* (Plate 6, ZD) is thought to mimic a braconine wasp. The larvae of the red and black *P. phlogina* tunnel in the bark of the woody climber *Ventilago viminalis* (Rhamnaceae) in inland Qld. *Hieromantis* (2 spp.) and *Calicotis* (4 spp.) have the scape forming an eye-cap. Most Australian species belong to *Stathmopoda* (60 spp.), in which the abdomen is spined dorsally. The larvae of *S. chalcotypa*, *S. cephalaea* and *S. callichrysa* (Fig. 41.40F) tunnel in rust galls on *Acacia decurrens*, and *S. crocophanes* has been reared from a loquat (*Photinia*) fruit. *S. melanochra* larvae are predators on *Eriococcus* scales on *Eucalyptus*, and those of *S. arachnophthora* feed in spider egg-sacs.

XYLORYCTINAE are well developed in Australia, where species of up to 75 mm wing expanse occur; in most species  $Rs$  and  $M_1$  of the hind wing are stalked or arise from the same point (Fig. 41.42C). The adults are seldom



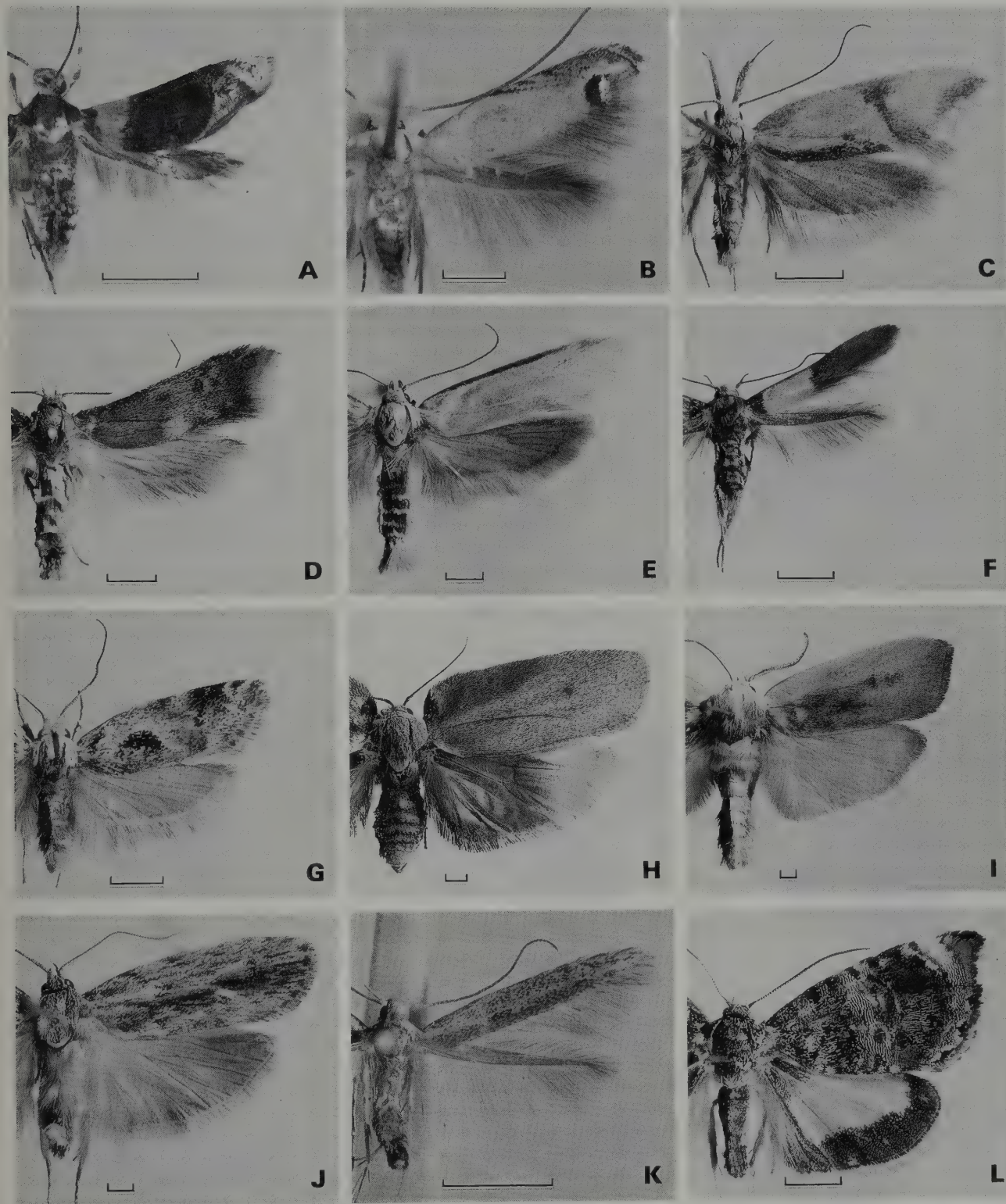


Fig. 41.40 A, *Epicroesa ambrosia*, Heliodinidae; B, *Leucoptera* sp., Lyonetiidae; C, *Thema chlorochyta*, D, *Hippomacha callista*, E, *Philobota productella*, F, *Stathmopoda callichrysa*, G, *Lichenaula choriodes*, H, *Uzucha humeralis*, I, *Cryptophasa rubescens*, J, *Agriophara platyscia*, Oecophoridae; K, *Batrachedra microtoma*, Batrachedridae; L, *Hypertropha tortriciformis*, Hypertrophidae. Scales: A, C–L = 2 mm; B = 1 mm. [C. Lourandos, E. Slater]

seen during the day, but come to light at night. Many are distinctively marked, and some are sexually dimorphic. The larvae feed on lichens, join leaves of angiosperms, feed in shelters beneath loose bark or tunnel in bark, flower spikes or the stems of trees, often cutting off leaves and attaching them at the entrance to the tunnel for later consumption.

The maxillary palps have 4 segments in most genera, including *Lichenaula* (56 spp.), *Scieropepla* (17 spp.), *Chalarotona* (1 sp.), *Telecrates* (4 spp.), *Catoryctis* (20 spp.) and *Uzucha* (2 spp.). The larvae of some, such as *L. choriodes* (Fig. 41.40G) and *L. lichenea*, feed upon lichens growing on fences and rocks, sheltering in a gallery of silk and refuse particles. *Scieropepla* larvae

tunnel in flower spikes, usually of *Banksia*, but those of *S. typhicola* burrow among the seeds of *Typha*. *Banksia* flower spikes are also tunnelled by larvae of *Chalarotona intabescens*. *Telecrates laetiorella* (Plate 7, H) larvae form a webbing gallery and feed on the inner bark of *Eucalyptus*. A conspicuous gallery of silk and bark particles is constructed by the larva of *Uzucha humeralis* (Fig. 41.40H), which feeds on the surface of the bark of *Angophora* and smooth-barked *Eucalyptus*. The adult has the base of the costa in the fore wing strongly arched, very short labial palps, and smoothly scaled hind tibiae.

In *Xylorycta* (100 spp.) the maxillary palps are 3-segmented, and the male antennae are ciliated. Many of the species are shining white. The larva of *X. luteotac-*

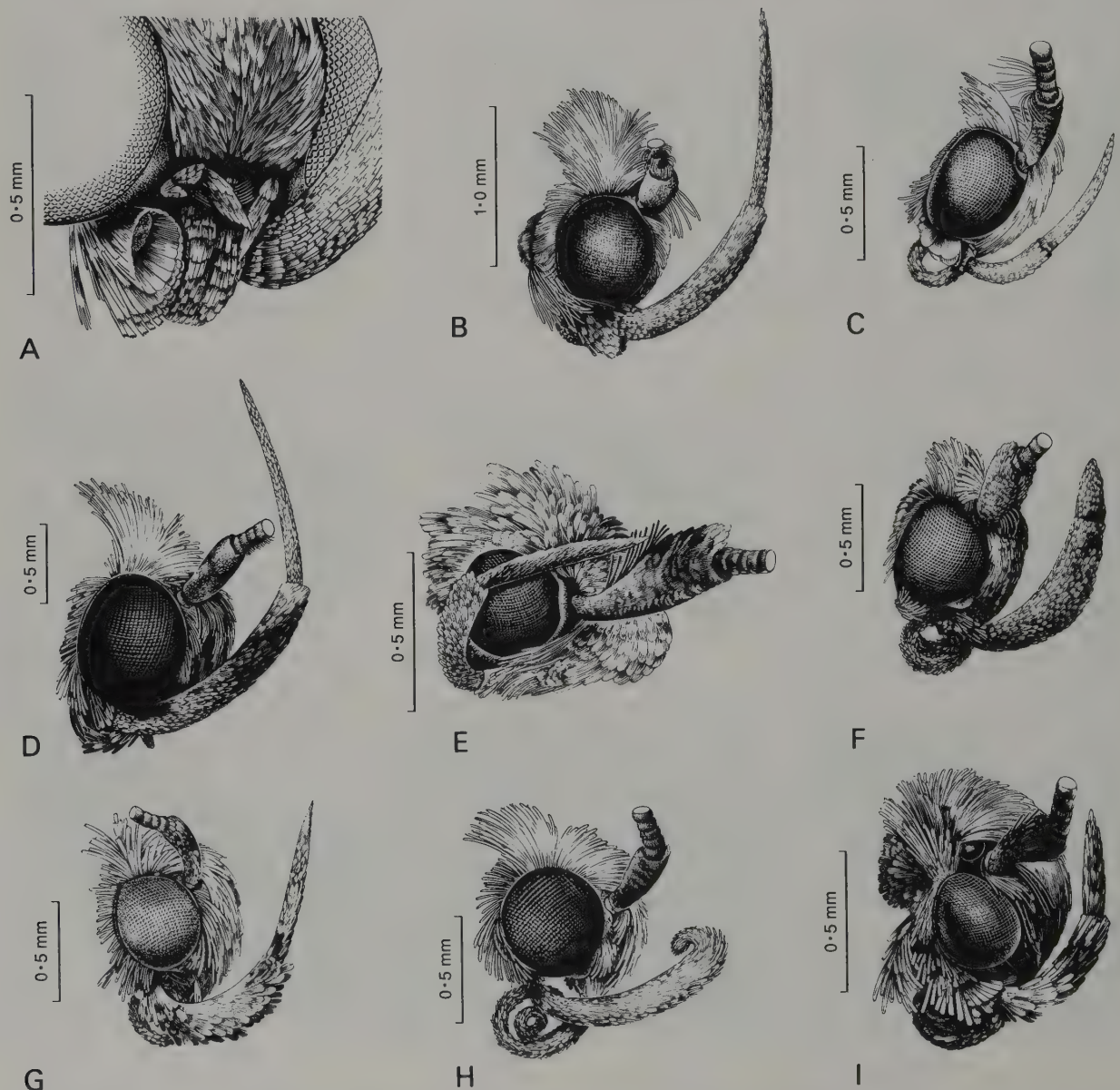


Fig. 41.41 Heads, lateral, of Gelechioidea: A, anterolateral view showing maxillary palps of Oecophoridae; B, *Philobota*, C, *Stathmopoda*, D, *Xylorycta*, Oecophoridae; E, *Agonoxena*, Agonoxenidae; F, *Blastobasis*, Blastobasidae; G, *Phthorimaea*, Gelechiidae; H, *Crocanthes*, Lecithoceridae; I, *Scythris*, Scythrididae.

[F. Nanninga]



*tella* lives either in a webbing shelter among twigs and leaves or in a short tunnel in a twig or the woody fruits of Proteaceae, including *Banksia* and *Hakea*, and is a pest of *Macadamia*. *X. strigata* is white with a broad fuscous longitudinal stripe on the fore wing. The larva tunnels in the branches of *Banksia serrata*, *B. integrifolia* and *Lambertia formosa*, feeding on leaves which it drags to the entrance of the tunnel. This habit is common in *Cryptophasa* (19 spp.), which contains the giants of the family, with maxillary palps of 3–4 segments and male antennae usually bipectinate. *C. rubescens* (Fig. 41.40i) tunnels in the stems of *Acacia*, covering the entrance with a web of silk, and feeding on phyllodes it drags to the tunnel. By contrast, the large *Maroga melanostigma* feeds on the bark of many native and exotic trees, often ring-barking them. Its main native host is *Acacia*, but it attacks citrus, stone and pome fruits, figs and ornamentals.

AUTOSTICHINAE are represented in Australia by three genera distinguished from Xyloryctinae and Gelechiidae by the genitalia. *Procometis* (20 spp.) bears a pencil of long hair-scales on the costa of the hind wing in the male. The larvae of *P. bisulcata* form a vertical tunnel in the soil, emerging at night through a flexible, silken, soil-encrusted tube to feed on terrestrial lichens, pieces of which are stored in a rounded chamber just beneath the soil surface.

The STENOMATINAE are numerous in the Neotropical region, but are represented in the Old World by *Agriophara* (31 Australian spp.) and a few smaller genera. Sc+R<sub>1</sub> of the hind wing approaches Rs towards the end of the cell (Fig. 41.42D) and the abdomen is without dorsal spines. The larvae of *Agriophara* at first excavate linear mines in *Eucalyptus* or *Lophostemon* leaves, later feeding between joined leaves. The pupae are found in a shelter

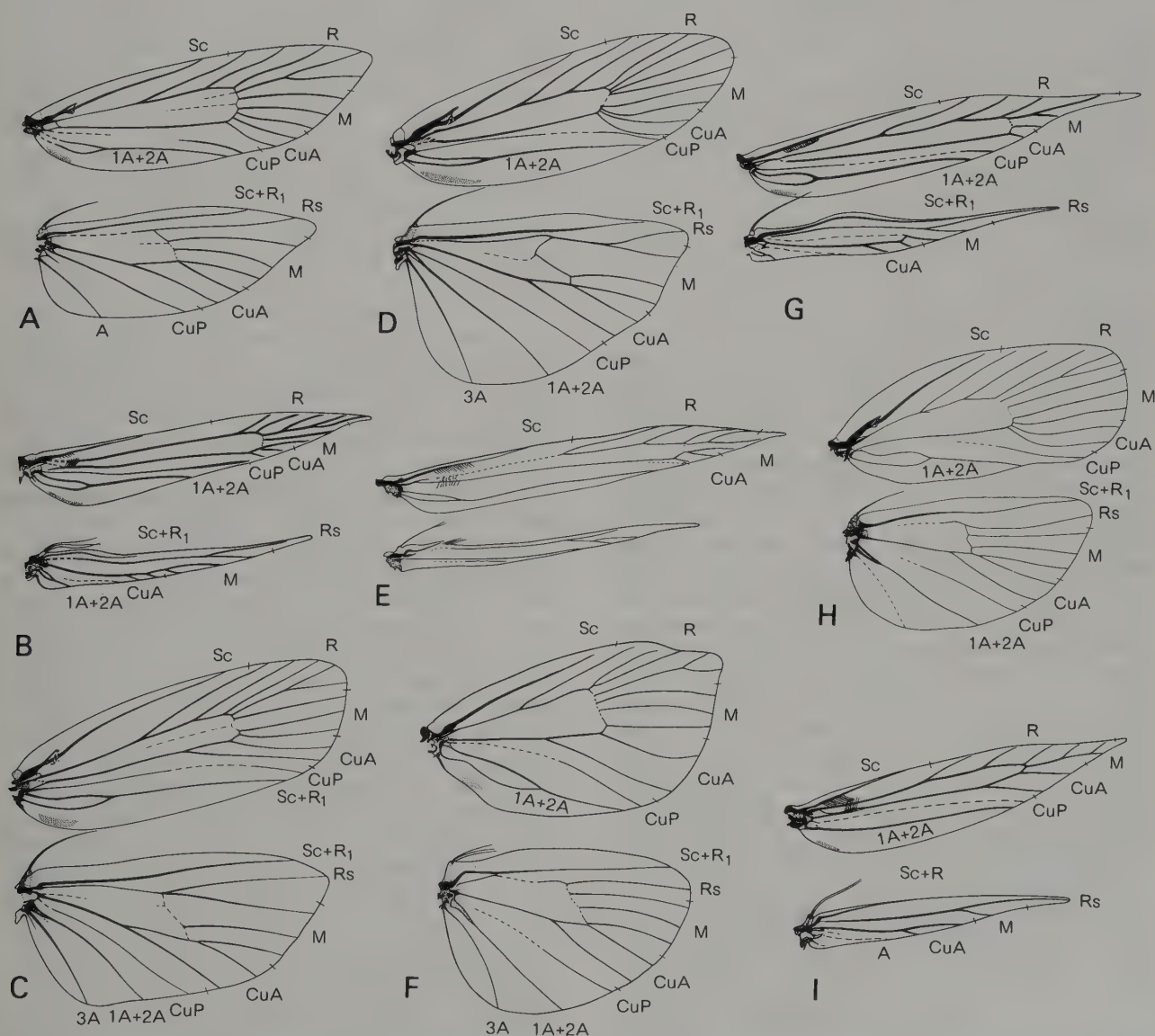


Fig. 41.42 Wing venation of Gelechioidea: A, *Philobota*, B, *Stathmopoda*, C, *Xylorycta*, D, *Agriophara*, Oecophoridae; E, *Batrachedra*, Batrachedridae; F, *Hypertropha*, Hypertrophidae; G, *Coleophora*, Coleophoridae; H, *Peritornenta*, Depressariidae; I, *Elachista*, Elachistidae.

[A–D, G, I by J. Wedgbrow; E, F, H by I. F. B. Common]

between fallen leaves, and can produce a clearly audible, stridulatory sound as they wriggle the abdomen and rub together the dentate margin of adjacent segments. *A. platyscia* (Fig. 41.40i) is one of many cryptic, grey species. [Duckworth 1973; Common 1977]

**28. Batrachedridae** (Fig. 41.40k). Very small; head smooth scaled; ocelli absent; antennae filiform; maxillary palps very small, sometimes folded over base of proboscis; labial palps recurved or drooping; epiphysis present, hind tibiae with piliform scales above; fore wing lanceolate (Fig. 41.42e), without pterostigma, 1 or 2 veins usually absent, CuP vestigial; hind wing linear, cell open, 1 branch of M absent, CuA a simple vein close to inner margin; frenulum in female with 2 bristles; T1–7 or 2–7 each with 2 elongate patches of spines, usually partly or wholly covered by scales; male genitalia symmetrical, uncus tapering, gnathos arms uniting medially, valva elongate, narrow, juxta with lateral lobes. Larva without secondary setae, crochets uniordinal in a circle. Pupa with maxillary palps, labial palps and fore femora exposed, abdomen with long dorsal setae.

The family was associated with the Coleophoridae by Hodges (1978). The best-known genus is *Batrachedra* (35 spp.). The larvae of *B. arenosella* prey on scale insects, feed beneath a silk webbing, and pupate in a flat, elliptical cocoon. They have also been reported feeding on the seeds of *Juncus* and other plants, but these records probably refer to other species.

**29. Hypertrophidae** (Fig. 41.40L). Small; head smooth scaled; ocelli absent; antennae filiform, scape without pecten; maxillary palps 4-segmented, folded over base of proboscis; labial palps recurved, short; epiphysis present; fore and mid tibiae and tarsi thickened with scales, hind tibiae with long piliform scales above and beneath; fore wing (Fig. 41.42F) often broad, sometimes with pterostigma, and slightly raised tufts of metallic scales or metallic terminal spots; R<sub>4</sub> and R<sub>5</sub> stalked or fused, CuP present; hind wing with Rs and M<sub>1</sub> nearly parallel, CuP present; frenulum in female with 2–4 bristles; abdomen without dorsal spines; male genitalia with uncus reduced to a pair of hairy lobes or absent, gnathos absent, sacculus of valva with discrete triangular sclerite at apex. Larva with some secondary setae in SV group and sometimes in L group on A9, crochets in irregular biordinal circle. Pupa exposed, upright, attached by hooked setae on ventral rounded lobes of A9, and small hooked setae on truncate end of A8–9.

Except for two species in New Guinea, the family is restricted to Australia. The adults rest with their wings folded steeply roofwise, with their thickened fore tibiae and tarsi extended in front. The larvae all feed on the green leaves of Myrtaceae. In *Eupselia* (16 spp.) the larvae are at first leaf-miners in *Eucalyptus*, later using the mine as a shelter while they feed on the adjacent leaf tissue. *E. satrapella* is one of a complex of similar species with orange and fuscous wings. The larvae of *Hypertrophia* (4 spp.) form a tubular network shelter of silk and faecal pellets on the under side of *Eucalyptus* or *Angophora* leaves, emerging to feed on the surrounding leaf. The pupa resembles the withered stub of a twig (Fig.

41.46A). *H. tortriciformis* (Fig. 41.40L) has metallic markings on the fore wing, with orange and black hind wings. [Common 1980]

**30. Depressariidae** (Figs 41.44B, C). Small to medium sized; head smooth scaled; ocelli usually absent; antennae usually filiform, occasionally bipectinate, scape with or without pecten; maxillary palps 4-segmented, folded over base of proboscis; labial palps recurved, 2nd segment sometimes porrect and expanded with scales; epiphysis present, hind tibiae with piliform scales above; fore wing (Fig. 41.42H) broad, without pterostigma, R<sub>2</sub> and R<sub>3</sub> sometimes stalked, R<sub>4</sub> and R<sub>5</sub> stalked, CuP present; hind wing usually broader than fore wing, Rs and M<sub>1</sub> parallel or connate, CuP present. S2 with long and slender apodemes and reduced rods; abdomen rarely with dorsal spines; male genitalia usually without uncus, gnathos usually with 1, 2 or 4 spinose knobs. Larva without secondary setae, crochets in bi- or triordinal circle. Pupa (Fig. 41.45D) short, stout, sometimes with smooth, sclerotised cuticle and formed in larval shelter, or variously formed and exposed, attached upright by hooked setae around margin and on truncate end.

The family is richly developed in the Northern Hemisphere, but only moderately so in Australia, where some species are restricted to rainforest, and others occur widely in sclerophyll forest or in alpine heathland in Tas. above 1000 m. Some genera, such as *Pedois* (14 spp.), *Tonica* (2 spp.) and *Peritornenta* (7 spp.), have a semi-erect, naked pupa with truncate abdomen attached to a pad of silk. The gnathos in the male is usually spinose. The larvae are usually leaf-tiers, but *Tonica effractella* (Fig. 41.44B), from northern Australia, tunnels in the stems of cotton and of *Brachychiton* and *Sterculia*. The larvae of *Peritornenta circulatella* from northern and eastern Australia feed between joined leaves of *Cupaniopsis* and *Atalaya*.

**31. Coleophoridae** (Fig. 41.44A). Very small; head smooth scaled; ocelli absent; scape with scale tuft or pecten; maxillary palps minute, 1- to 4-segmented; labial palps long, recurved; epiphysis sometimes reduced or absent; hind tibiae usually with long piliform scales; fore wing (Fig. 41.42G) lanceolate, without transverse markings and rarely with pterostigma, at least 1 vein absent; hind wing linear-lanceolate, usually at least 1 vein absent; female with frenulum of 1 bristle; T1–7 each with 2 elongate patches of spines not concealed by scales; valva in male partly divided, gnathos elongate, with spinose apical knob. Larva in 1st instar with ventral prolegs sometimes absent, but anal prolegs present; in later instars prolegs may be absent from segment 6, or from 3–6; a leaf-miner in 1st instar, then a case-bearer, feeding externally on leaves or flowers, or mining in leaves. Pupa (Fig. 41.45E) with maxillary palps absent, labial palps and fore femora exposed, in larval case.

The adults rest with antennae porrect. The larvae of the endemic *Corythangela* from eastern N.S.W. feed on *Casuarina* in an elongate case of pieces of the branchlets. Other endemic species are referred to *Coleophora*, and little is known about their early stages. An unnamed *Coleophora* (Fig. 41.44A) with grey wings and veins out-



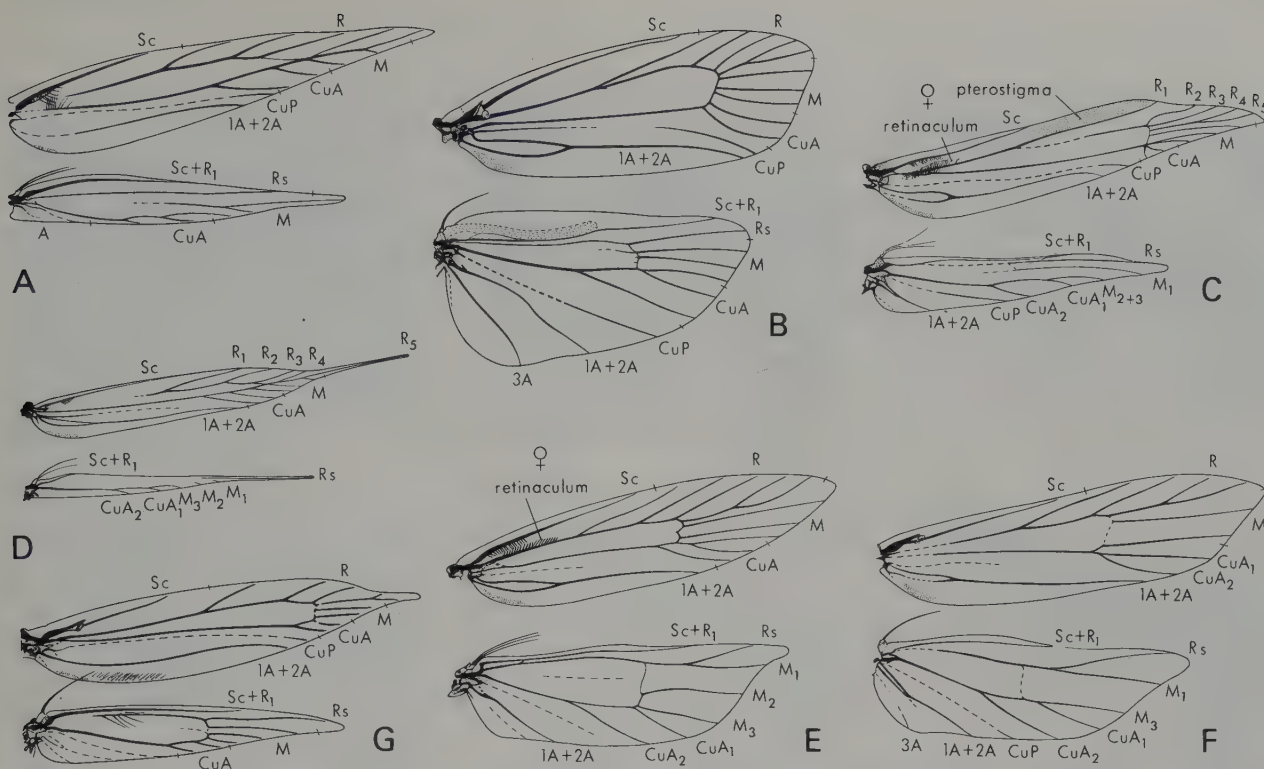


Fig. 41.43 Wing venation of Gelechioidea: A, *Agonoxena*, Agonoxenidae; B, *Ethmia*, Ethmiidae; C, *Blastobasis*, Blastobasidae; D, *Cosmopterix*, Cosmopterigidae; E, *Stegasta*, Gelechioidea; F, *Crocanthes*, Lecithoceridae; G, *Scythris*, Scythrididae. [J. Wedgborough]

lined with ochreous has been reared from larvae feeding on *Rutidosia*. *C. serinipennella* makes galls in the stems of Chenopodiaceae in inland N.S.W. The bronzy green *C. alcyonipennella* from Europe is established in south-eastern Australia, Tas. and New Zealand, where the larva feeds on the flowers of white clover, greatly reducing seed production. [Vives Moreno 1988]

**32. Elachistidae** (Fig. 41.44D). Very small; head smooth scaled; ocelli present or absent; scape sometimes with pecten; proboscis rarely vestigial; maxillary palps 1- or 2-segmented; labial palps recurved, porrect or drooping; hind tibiae usually with long hair-scales; fore wing (Fig. 41.42i) lanceolate,  $R_5$  to costa; hind wing lanceolate,  $Sc+R_1$  remote from  $R_s$  which extends in a nearly straight line through or near axis of wing, cell usually closed; female with frenulum of 2 bristles; abdomen rarely with dorsal spines; gnathos usually with 1 or 2 spinose knobs. Larva with crochets uniordinal, rarely biordinal, in complete or broken circle, or transverse bands; leaf- or stem-miners, usually in grasses or sedges. Pupa usually with protuberances and exposed, abdomen without movement, attached by cremaster and central girdle, sometimes in flimsy cocoon.

The adults can usually be recognised by the axial condition of  $R_s$  of the hind wing, and the spinose gnathos in the male. The larva of *Cosmiotes synethes* (Fig. 41.44d) pupates in a flimsy cocoon. It mines in the leaves of grasses, and has been reared from wheat. The known pupae of Australian species referred to *Elachista* are without a cocoon. [Traugott-Olsen and Nielsen 1977]

**33. Agonoxenidae** (Fig. 41.44E). Very small; head (Fig. 41.41E) smooth scaled; ocelli absent; frons very oblique; scape without pecten; maxillary palps 1-segmented; labial palps recurved, apical segment flattened; epiphysis present, hind tibiae with long hair-scales; fore wing (Fig. 41.43A) lanceolate, without pterostigma,  $R_5$  and  $M_1$  stalked,  $R_5$  to costa, 1 vein absent, CuP present; hind wing linear-lanceolate,  $Sc+R_1$  remote from  $R_s$ ,  $R_s$  and  $M_1$  remote,  $M_3$  to  $CuA_2$  very short, or 2 veins absent, discal cell open; female with frenulum of 2 bristles; abdomen without dorsal spines; gnathos a spinose knob; signum a pair of dentate patches. Larva with crochets irregularly uniordinal in a circle, some secondary setae in SV group; beneath a flimsy, silken web. Pupa flattened, antennae exceeding end of wings, abdominal segment 9 with pair of ventral leg-like processes, each with a series of short, apical setae; within double-walled, silken cocoon.

The reduced maxillary palps, the position of  $R_s$  in the hind wing, the female frenulum, and the male genitalia indicate a relationship to less specialised species of Elachistidae. The larva of *Agonoxena phoenicia* (Fig. 41.44E), from northern Qld, feeds beneath the leaves of the palm *Archontophoenix alexandrae*, and pupates in a fusiform, white, silken cocoon spun in the larval shelter. The related *A. argaula* is a pest of coconut palms in Fiji and other Pacific islands. The adult runs rapidly, and rests with the wings tightly folded along the body, the antennae porrect, and the fore legs extended in front. [Bradley 1966]

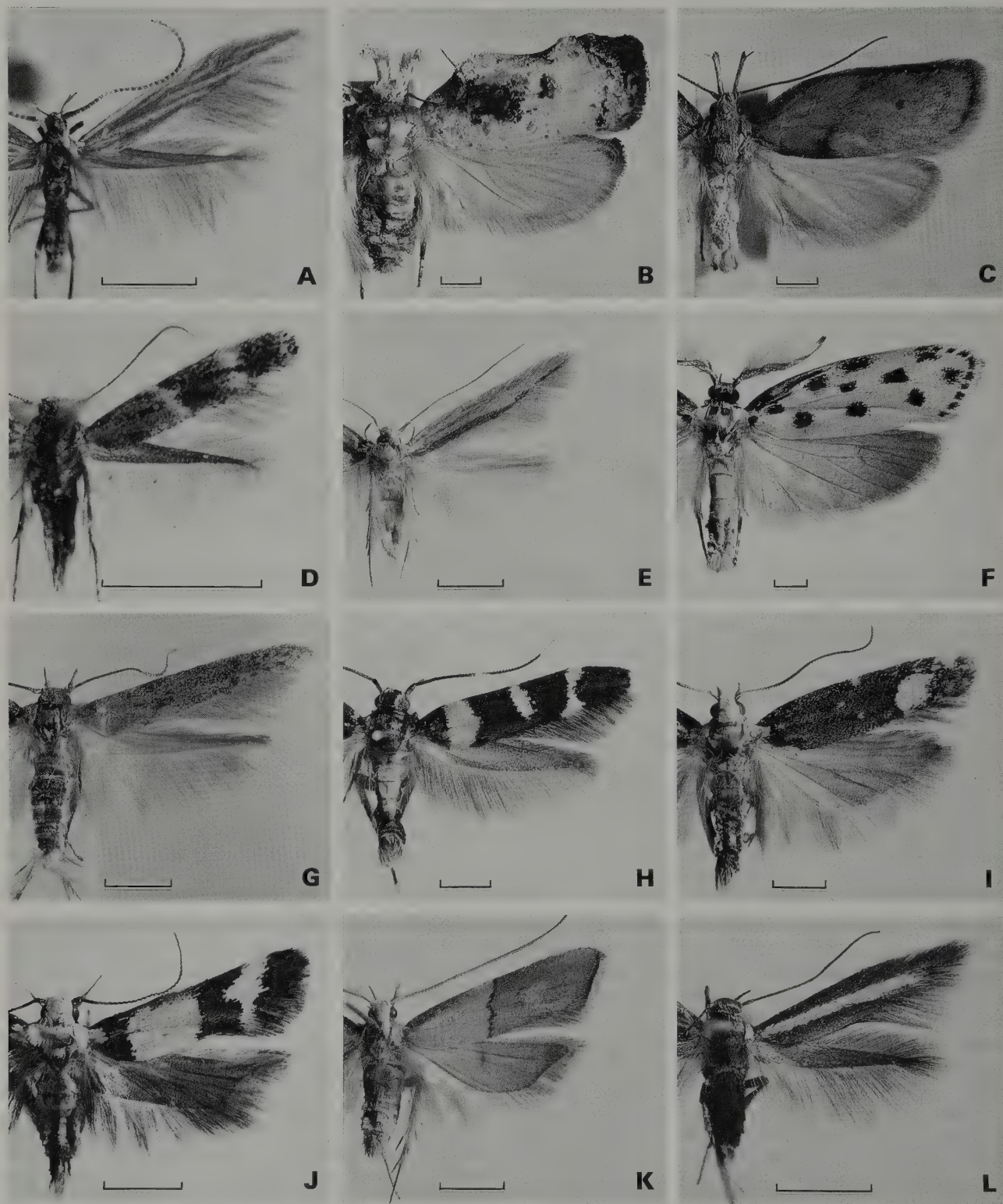


Fig. 41.44 A, *Coleophora* sp., Coleophoridae; B, *Tonica effractella*, C, *Enchocrates glaucopsis*, Depressariidae; D, *Cosmiotes synethes*, Elachistidae; E, *Agonoxena phoenicia*, Agonoxenidae; F, *Ethmia sphaerosticha*, Ethmiidae; G, *Blastobasis sarcophaga*, Blastobasidae; H, *Limnaecia cirrhizona*, Cosmopterigidae; I, *Protolechia deltodes*, J, *Decatopseustis xanthastis*, Gelechiidae; K, *Crocantes prasinopis*, Lecithoceridae; L, *Scythris rhabducha*, Scythrididae. Scales = 2 mm.

[C. Lourandos, E. Slater]



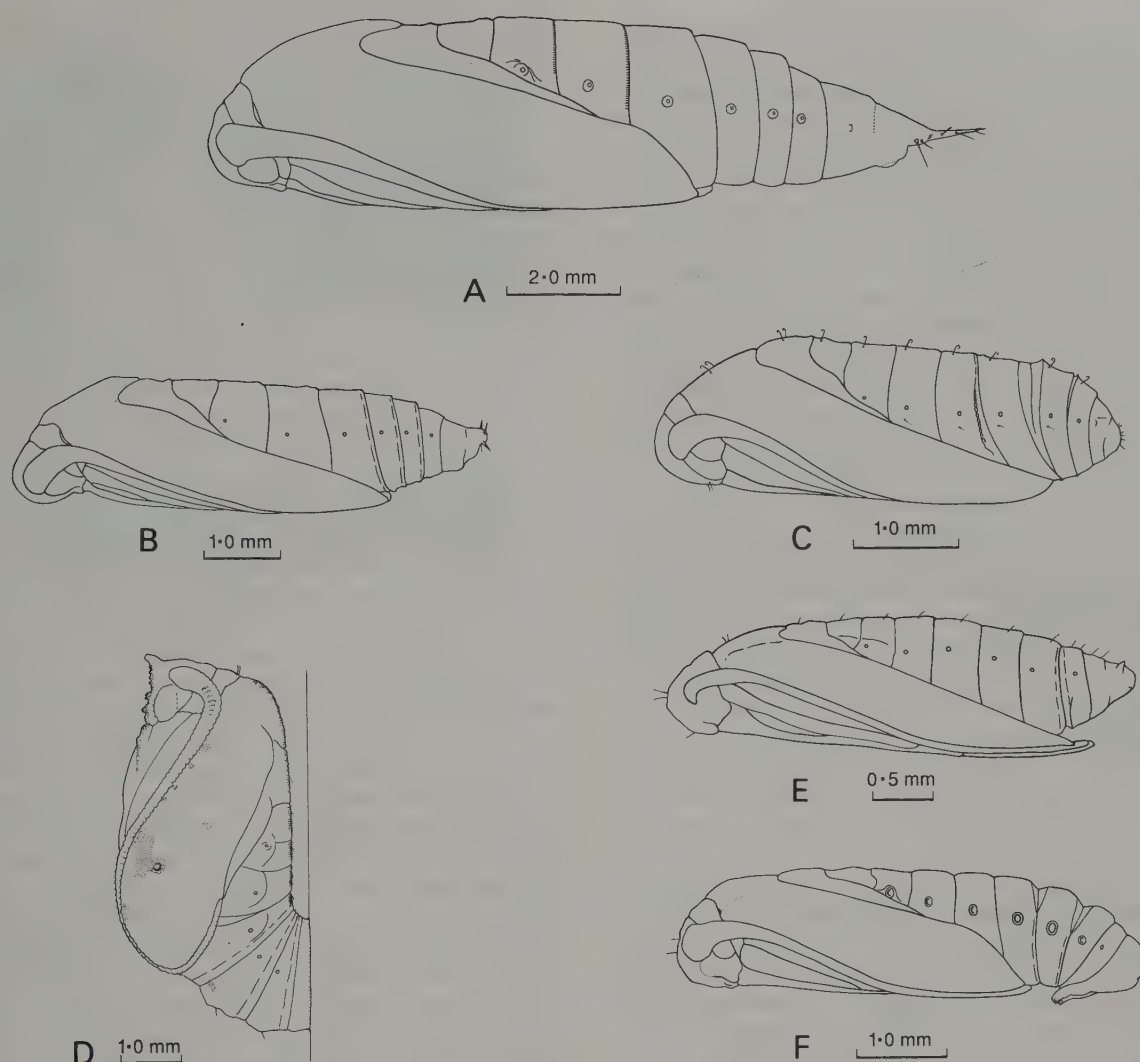


Fig. 41.45 Pupae of Gelechioidea: A, *Garrha*, B, *Stathmopoda*, Oecophoridae; C, *Blastobasis*, Blastobasidae; D, *Peritormenta*, Depressariidae; E, *Coleophora*, Coleophoridae; F, *Ethmia*, Ethmiidae.  
[I. F. B. Common]

**34. Ethmiidae** (Fig. 41.44F). Small to medium sized; head smooth scaled; ocelli absent; antennae usually without pecten on scape; maxillary palps usually 4-segmented, folded over base of proboscis; labial palps recurved; epiphysis present; hind tibiae with long filiform scales; fore wing (Fig. 41.43B) without pterostigma,  $R_4$  and  $R_5$  stalked,  $R_5$  to costa or apex, CuP present at least towards margin; hind wing with  $R_s$  and  $M_1$  well separated at base, divergent,  $M_2$  not arising nearer to  $M_3$  than to  $M_1$ , CuP present; frenulum in female with 3 bristles; abdomen not spined; male genitalia with uncus often bifurcate or reduced, gnathos sometimes absent, valva usually deeply divided. Larva usually with some secondary setae at least in SV groups, crochets in bi- or uniordinal circle, mesoseries or mesal penellipse; usually beneath light webbing on Boraginaceae. Pupa with a pair of ventral, leg-like processes on abdominal segment 9, each with a series of hooked apical setae (Fig. 41.45F).

In Australia the family is mainly tropical. The species resemble Oecophoridae, but are distinguished by the

characteristic male genitalia, usually by the position of  $M_2$  in the hind wing, and by the ventral abdominal processes of the pupae. The fore wings often have bold black spots on a white or grey background. In the rainforest species, *Ethmia sphaerosticha* (Fig. 41.44F), the male antenna bears an expandable tuft of long, silky hairs; the larva, which feeds on the leaves of *Ehretia* (Boraginaceae), lacks secondary setae. In other *Ethmia* (13 spp.) the antennae are filiform in both sexes. *E. thoraea*, with grey fore wings and orange hind wings, has a small pecten on the scape. *E. clytodoxa* and *E. hemadelpha* are black-spotted white species. Larvae of the latter feed in northern Australia on *Ehretia saligna*. *E. heliomela*, with bronzy black fore wings and orange hind wings, lacks conspicuous spots; its larvae feed on *Ehretia acuminata* and sometimes cause defoliation. [Powell 1981, 1985]

**35. Blastobasidae** (Fig. 41.44G). Very small; head (Fig. 41.41F) smooth scaled; ocelli absent; scape often dilated and concave beneath, with dense pecten or tuft of scales, 1st flagellar segment with basal notch in males of

several genera; maxillary palps 4-segmented, folded over base of proboscis, or 1- or 2-segmented; labial palps usually recurved, in male often flattened, thick and blunt apically; epiphysis present, hind tibiae with long filiform scales above; fore wing (Fig. 41.43C) lanceolate, pterostigma present,  $R_2$  arising near upper angle of discal cell, base of  $CuA_2$  usually perpendicular to  $CuA$ ,  $CuP$  present near margin; female retinaculum of specialised scales arising from bases of  $R$  and  $CuA$ ; hind wing lanceolate,  $Sc+R_1$  fused with  $Rs$  near base; abdomen with dorsal spines; male genitalia with divided valvae. Larva without secondary setae, with crescent-shaped pigmented area around  $SD1$  on  $A1$  to  $A7$ , crochets uni- or biordinal in circle; feeding on fallen woody fruits, seeds, reproductive parts of cycads and dry refuse, rarely on aphids and scale insects. Pupa (Fig. 41.45C) stout.

The family has a world-wide distribution; at least 2 genera and at least 20 species (almost half of which are undescribed) occur in Australia, mostly in the north-east. The dull grey moths may be recognised by the pterostigma and position of  $R_2$  in the fore wing, and the fusion of  $Sc+R_1$  and  $Rs$  in the hind wing. The specialised subradial and subcubital retinaculum of the female is not found elsewhere. *Blastobasis tarda* has a broadly dilated scape, dense pecten, and blunt apical segment of the labial palps in the male. *B. sarcophaga* (Fig. 41.44G), the larvae of which tunnel in fallen palm fruits, has a sparse pecten and the labial palps of the male are normal. [Adamski and Brown 1989]

**36. Cosmopterigidae** (Fig. 41.44H). Very small to small; head smooth scaled; ocelli present or absent; antennae simple or ciliated, scape long and slender, pecten sometimes present; maxillary palps 4-segmented, folded over base of proboscis; labial palps long, recurved; epiphysis present, hind tibiae with long hair-scales; fore wing (Fig. 41.43D) lanceolate, without pterostigma,  $R_2$  arising well before end of discal cell,  $R_4$  and  $R_5$  stalked,  $R_5$  to costa,  $CuP$  vestigial or absent; hind wing linear or lanceolate,  $Sc$  separate from  $Rs$ ,  $R_1$  sometimes present, discal cell sometimes open, venation often reduced; frenulum in female with 3 bristles; abdomen without dorsal spines; male genitalia often asymmetrical, either uncus or gnathos absent; gnathos when present asymmetrical, aedeagus fused to juxta or to saccus; female sometimes with piercing ovipositor. Larva with crochets uni- or biordinal in circle; mining in leaves, boring in stems, seeds or fungi, tying leaves, forming galls, or predatory on scale insects. Pupa with maxillary palps small or absent, labial palps and fore femora concealed, cremaster sometimes present, with straight or hooked setae.

The family (Hodges 1978) contains 3 subfamilies, Antequerinae, Cosmopteriginae and Chrysopeleiinae, the first of which has not been recorded from Australia.

COSMOPTERIGINAE have asymmetrical male genitalia, without an uncus and with the aedeagus fused to the juxta. The fore wing is without tufts of raised scales. *Cosmopterix* (10 spp.) contains minute, blackish species with orange and bright metallic markings. The larvae mine in leaves of grasses and other plants. *C. mimetis* occurs north from Sydney. *Limnaecia* (53 spp.) often has

blackish fore wings and transverse white or orange markings, as in *L. cirrhozona* (Fig. 41.44H). *L. phragmitella* is a slender, ochreous species with larva burrowing among the seeds of *Typha angustifolia*. In *Labdia* (20 spp.) the hind wings are narrower. *L. leucombra* is one of several species with delicate stripes on the fore wing. The pink larvae of *Pyroderces rileyi* are scavengers in damaged cotton bolls and sorghum heads in northern Australia and North and South America.

CHRYSOPELEIINAE have asymmetrical or symmetrical male genitalia, with the aedeagus fused to the saccus, and with an uncus present. The fore wing often has tufts of raised scales. The ovipositor sometimes is modified for piercing plant tissues. The larvae of the blackish *Chalotis semnostola* mine in the tips of the young phyllodes of *Acacia implexa* and other wattles. An introduced North American species, *Ithome lassula*, damages the florets and affects seed-setting in the fodder legume *Leucaena leucocephala* (Common and Beattie 1982).

**37. Gelechiidae** (Plate 7, K; Figs 41.44I, J) Small; head (Fig. 41.41G) smooth scaled; ocelli often present; antennae simple or shortly ciliated, scape seldom with pecten; maxillary palps 4- or rarely 3-segmented; folded over base of proboscis; labial palps recurved, 2nd segment often tufted beneath or rough scaled; epiphysis present, hind tibiae with long hair-scales; fore wing (Fig. 41.43E) without pterostigma,  $R_4$  and  $R_5$  usually stalked,  $R_5$  to costa,  $CuP$  absent, female retinaculum a row of curved specialised scales on  $R$ ; hind wing usually more or less trapezoidal, with termen sinuate or emarginate,  $CuA$  sometimes with basal pecten,  $R_1$  present,  $Rs$  and  $M_1$  usually approximated at base or stalked,  $M_3$  and  $CuA_1$  connate or stalked, rarely separate,  $CuP$  usually absent; abdomen rarely with dorsal spines. Male genitalia with uncus broad or slender, gnathos usually a hook or elongate and tapering, valvae usually long and slender, aedeagus usually bulbous. Larva rarely with secondary setae on prolegs, occasionally with anal fork, crochets uni- or biordinal, in circle, mesal pen-ellipse or in 2 transverse rows, rarely reduced or absent; joining leaves, feeding on seeds, or mining in leaves or stems; rarely in portable case. Pupa with maxillary palps present, labial palps and fore femora concealed, cremaster sometimes present; in silken cocoon in larval shelter or among detritus on ground.

Though numerous in Australia, the Gelechiidae are greatly outnumbered by the Oecophoridae. Most genera may be recognised by the trapezoidal hind wing, usually with emarginate termen, and by the condition of  $Rs$  and  $M_1$  in the hind wing. In *Protolechia* the hind wing is not trapezoidal,  $Rs$  and  $M_1$  are nearly parallel, and the abdominal terga are minutely spinose anteriorly. All Australian genera lack  $CuP$  in both wings, and have the specialised retinaculum in the female. Hodges (1986) recognised three subfamilies: Gelechiinae, Pexicopiinae and Dichomeridinae.

*Anarsia* (7 spp.), *Dichomeris* (20 spp.) and *Xerometra* (1 sp.) have a large, ventral scale-tuft on the 2nd segment of the labial palps. In *Anarsia* the apical segment is very short in the male, whereas it is of normal length in the female. The larvae feed between leaflets or in galls on



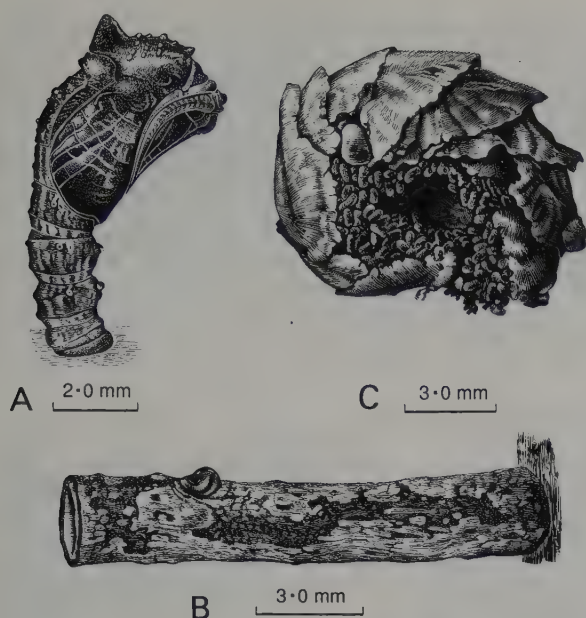


Fig. 41.46 Pupa and larval cases of Gelechioidea: A, pupa of *Hypertropha*, Hypertrophidae; B, C, larval cases of *Hippomachia* and *Aristeidae*, Oecophoridae. [F. Nanninga]

*Acacia*. *Anarsia molybdota* occurs widely in the south. The adults of *Dichomeris* are sombre insects found in leaf litter in the denser eastern forests. The larvae of *D. capnites* feed on the foliage of *Acronychia*, and the adults sometimes occur in vast numbers. *D. ochreoviridella* (Plate 7, K) occurs widely in northern Australia. The widely distributed *Xerometra crocina* is common in eastern Australia, the larvae feeding in the seed pods of legumes. The largest endemic genus is *Protolechia* (139 spp.), with larvae feeding between joined leaves, usually of *Eucalyptus*. Pupation occurs in a silk-lined cell between fallen leaves, and the cryptic adults rest on *Eucalyptus* trunks. *P. aversella* occurs widely in the south, while *P. deltodes* (Fig. 41.44i) is found in Vic. and N.S.W.

*Phthorimaea* (1 sp.) and *Scrobipalpa* (5 spp.) include two pests of Solanaceae. *P. operculella* is a leaf-miner in tobacco and potatoes, and tunnels in potato tubers. *S. apatella* also attacks tobacco. *Symmetrischema plaesiosema* tunnels in stems of tomatoes. The larvae of *Pectinophora* (3 spp.) and *Pexicopia* (20 spp.) feed in the seed capsules of Malvaceae (Common 1958b). A pecten of at least 2 or 3 hair-scales is present on the scape in these genera. *Pectinophora gossypiella* damages cotton bolls in north-western Australia and the N.T., and *P. scutigera* is a minor cotton pest in Qld. *Hibiscus* is the native host plant. *Pexicopia nephelombra* flies commonly amongst *Sida* and other malvaceous weeds in sub-coastal Qld, often with the related *Decatopseustis xanthastis* (Fig. 41.44j) which lacks an antennal pecten. *Thiotricha* (18 spp.) contains slender, elegantly patterned, usually satin-white species, in which the male antennae have long cilia, and the fore wing lacks 2 veins. *T. parthenica* has ochreous yellow wings; its larva constructs a portable case of withered leaf particles, and bores into the lower surface of

the leaves of *Grevillea punicea*. In *Apatetris* (27 spp.) the scape has a strong pecten, the apical segment of the labial palps is very short, and the termen of the hind wing is deeply emarginate. The larva of *A. miarodes*, from the east coast, forms a linear mine in leaves of *Lomandra longifolia*, and pupates in a white cocoon in the leaf litter. A pecten is also present on the scape of *Sitotroga cerealella*, a cosmopolitan pest of stored grain.

**38. Lecithoceridae** (Timyridae) (Fig. 41.44k). Small; head (Fig. 41.41h) smooth scaled; ocelli absent; antennae often thickened in male, nearly as long as or longer than fore wing; maxillary palps 4-segmented, folded over base of proboscis; labial palps recurved, in male sometimes modified; fore wing (Fig. 41.43f) without pterostigma, with elongate area of long oblique setae near inner margin beneath, which probably interlocks with a subcostal series of setae on hind wing above;  $R_3$  and  $R_4$  or  $R_4$  and  $R_5$  stalked,  $R_5$  usually to costa,  $CuA_1$  and  $CuA_2$  usually stalked,  $CuP$  rarely present; hind wing with  $R_s$  and  $M_1$  connate or stalked,  $CuP$  present; venation may be reduced; abdomen often with dorsal spines. Male genitalia symmetrical, uncus present, gnathos distinctively shaped. Female sometimes with terminal tuft of deciduous scales. Larva with dense, branched, secondary setae arranged on verrucae, crochets in uniordinal, mesal penellipse or in 2 curved, transverse rows. Pupa with maxillary palps present, labial palps and fore femora exposed, cremaster present.

The presence of dense secondary setae in the larva sets the family apart from other Gelechioidea except Scythrididae, with which family it shares the presence of series of long, obliquely arranged setae beneath the fore wing and above the hind wing. The moths rest with head directed downwards and antennae held correct. Most species occur in the Oriental and Australian regions, being mainly tropical and subtropical. *Crocantthes* (25 spp.) contains bright yellow, orange or pink species with dorsally spined abdomen. The males of some species, such as *C. prasinopsis* (Fig. 41.44k), have segments 2 and 3 of the labial palps fused to form a long, weak, partly coiled segment (Fig. 41.41h). *Lecithocera* (65 spp.) includes dark species which shelter among the leaf litter. *L. micromela* from the south-east is common in dry, grassy places. [Gozmány 1978]

**39. Scythrididae**. Very small, head (Fig. 41.41i) smooth scaled; ocelli sometimes present; scape usually with pecten; maxillary palps 4-segmented; labial palps recurved, smooth scaled; epiphysis present, hind tibiae with long hair-scales; fore wing (Fig. 41.43g) lanceolate,  $R_1$  from beyond middle of discal cell but remote from  $R_2$ ,  $R_4$  and  $R_5$  stalked,  $R_5$  to termen, 1 or 2 veins absent,  $CuP$  present near margin; hind wing lanceolate,  $R_s$  and  $M_1$  parallel; frenulum in female with 2 or 3 bristles; abdomen without spines; male genitalia often asymmetrical and highly modified. Larva with most pinacula bearing secondary setae, crochets usually triordinal in a circle; spins silken webbing or gallery. Pupa with minute maxillary palps, labial palps exposed, fore femora concealed, wings extending to abdominal segment 7, spiracles tubular, setae mostly hooked.



Most Australian species are referred to *Scythris* (15 spp.) and *Eretmocera* (4 spp.). The adults of *Scythris* are blackish above and pale beneath, sometimes with a white, longitudinal stripe on the fore wing, as in *S. rhabducha* (Fig. 41.44L). Their larvae are not known, but the adults are sometimes common among grass or *Eucalyptus* leaf litter, flying in the late afternoon. *E. dioctis* has been reared from larvae on grasses. [Bengtsson 1984]

### Superfamily COSSOIDEA

Small to very large, usually robust; ocelli usually absent; chaetosemata absent; proboscis short and naked or absent;

maxillary palps minute; fore wing with chorda and M in cell; S2 of tortricoid type (S2 apodemes short, broad and not connected with sternal rods). Larvae stem- and wood-boring.

The families Cossidae and Dudgeoneidae are phenetically similar but no obvious synapomorphy has been identified. Because of the presence of tympanal organs in Dudgeoneidae this family has been placed with the Pyralidae (Minet 1983). Detailed studies of the distribution of tympanal organs within the superfamily are likely to improve our understanding of the interrelationships of cossoid family-groups.

### Key to the Families of Cossioidea Known in Australia

- Fore wing reddish brown with circular, silvery-white spots ..... **Dudgeoneidae** (p. 872)  
 Fore wing shades of grey or white, without silvery spots ..... **Cossidae** (p. 870)

**40. Cossidae** (wood moths, goat moths) (Figs 41.47A–D). Small to very large; head with raised, slender scales on vertex and often a tuft of converging scales on frons; ocelli usually absent; chaetosemata absent; antennae usually bipectinate, rarely lamellate or filiform in male, usually filiform or weakly pectinate in female; proboscis very short, naked or absent; maxillary palps minute, 1- or 2-segmented; labial palps short and straight or moderate and upturned; epiphysis rarely absent; spurs 0-2-4, 0-2-2 or absent. Fore wing (Figs 41.48A, B) elongate, strong, pterostigma rarely present, retinaculum on Sc or between costa and Sc, female frenulum of 2–30 bristles, females of some species brachypterous, with strong forked M in cell, chorda usually present, R<sub>3</sub> usually stalked with R<sub>4</sub> (and R<sub>5</sub>) to termen, CuP present; hind wing broad, M usually forked in cell, with 2 A veins, CuP sometimes reduced. Eggs of flat type in Zeuzerinae, upright with ribs in most Cossinae. Larva (Fig. 41.49A) stout, prothorax with large, dorsal, sclerotised, shield and 3 L setae; crochets usually in an ellipse, uni-, bi- or triordinal, wood-boring. Pupa (Fig. 41.49B) long, cylindrical and well sclerotised, head usually with spine; abdominal segments 3–7 movable in male, 3–6 in female, T2–7 in males and 2–6 in females each with 2 transverse rows of spines, T8 in male, T7 and 8 in female each with one row; cremaster absent; protruded from tunnel at ecdysis.

Largely because of the venation, the family has been regarded as one of the most primitive ditrysian groups. However, the chaetotaxy of the larvae, male genitalia and general biology and appearance suggest a close relationship with the Tortricidae. It is possible that the Cossidae and Tortricidae are among the earliest branches of the ditrysian lineage with tortricoid S2 apodemes (termed the Apoditrysia by Minet (1983)).

Australia has a rich and diverse cossid fauna (Turner 1945; Tindale 1953). Females lay their eggs singly, in pairs or in large numbers, inserting them into crevices, or depositing them on the food plant. The larvae bore in the heartwood or in the larger roots of living trees, shrubs or woody herbs, form galleries beneath bark, or rarely tunnel in soil, feeding externally on roots. Pupation occurs in a chamber within the tunnel.

COSSINAE have the male antennae bipectinate to the tip, hind wing with veins Rs and M<sub>1</sub> stalked or connate, hind tibiae swollen and usually with two pairs of spurs and gnathos with arms fused medially.

The red larvae of *Culama* (Fig. 41.47A; 4 spp.) live gregariously in galleries excavated beneath bark of *Eucalyptus* and *Angophora* and pupate in oval cocoons in the larval galleries or in the soil. *C. rhytiphorus* occurs widely in eastern Australia. *Macrocyttara expressa* (Fig. 41.47B) also has red larvae; these tunnel in the trunks and branches of the mangrove *Aegiceras corniculatum*.

The subfamily assignment of *Idioses* (1 sp.), *Charmoses* (1 sp.) and *Ptilomacra* (1 sp.) is uncertain. The larvae of *Ptilomacra senex* from eastern and south-eastern Australia bore in grass trees, *Xanthorrhoea*. *Idioses littleri*, from eastern Australia and Tas., differs in several characters from other Cossidae and may prove important for the understanding of the phylogeny of the family.

ZEUZERINAE have the male antennae bipectinate in not more than basal three-quarters, Rs and M<sub>1</sub> veins separate in hind wing, hind tibiae with one pair of spurs or without spurs, and gnathos with arms separate or absent. Species of *Xyleutes* (with over 100 species in Australia) range in wingspan from about 30 mm in males of *X. amphiplecta* (Fig. 41.47C) to about 230 mm in the females of *X. cinereus* and *X. affinis* (Fig. 41.47D), with abdomens measuring up to 70 mm in length and 22 mm in diameter. Vast numbers of eggs are laid; those deposited by a single female of one of the larger species, *X. encalypti*, exceeded 18 000. The mass of small yellowish eggs is covered with a glutinous secretion, beneath which the newly hatched larvae live for a day or two before dispersing. The 1st instar larvae spin great quantities of silk, and Kalshoven (1965) stated that they are dispersed by wind when they lower themselves on silken strands. The larvae of *X. encalypti* tunnel in the larger roots of *Acacia*, but many, such as *X. cinereus* and *X. affinis*, bore singly in the trunks of *Eucalyptus*, taking 2 and possibly 3 years to reach maturity. Faecal pellets ejected through a small opening betray the presence of a larva. Before pupation, the tunnel to the ejection hole is enlarged, and the bark covering is almost severed. Pupation takes place in the



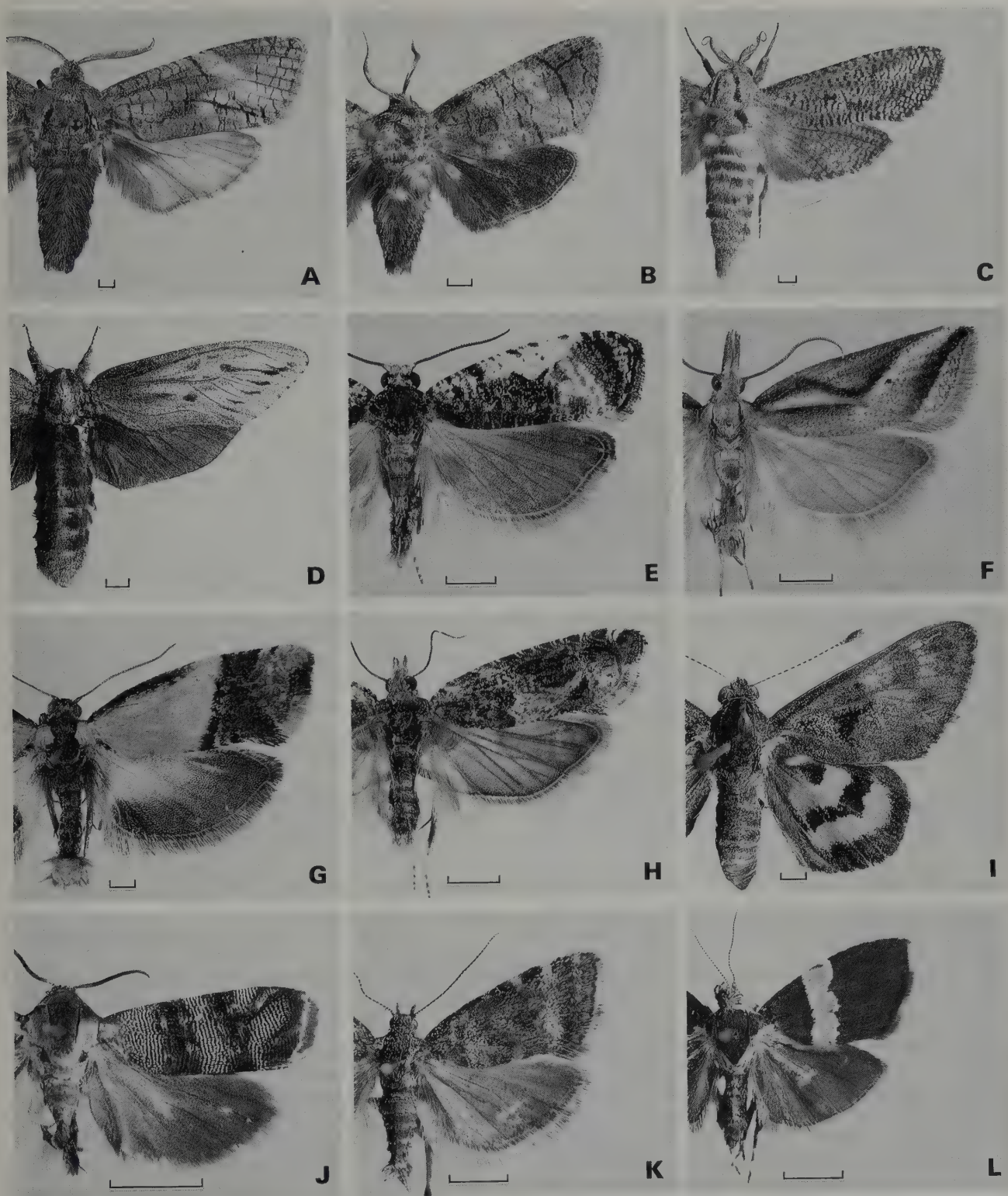


Fig. 41.47 A, *Culama australis*, B, *Macrocyttara expressa*, C, *Xyleutes amphiplecta*, D, *Xyleutes affinis*, Cossidae; E, *Phricanthes asperana*, F, *Arotrophora arcuatalis*, G, *Epitymbia cosmota*, H, *Crociosema plebejana*, Tortricidae; I, *Synemon laeta*, Castniidae; J, *Nigilgia adjectella*, Brachodidae; K, *Asterivora lampadias*, L, *Choreutis basalis*, Choreutidae. Scales: A–C, E–L = 2 mm; D = 10 mm.

[J. Green, E. Slater, C. Lourandos]

tunnel, sometimes in a chamber of chewed wood, and a felted pad which is usually fixed in the tunnel is pushed out by the emerging pupa before ecdysis. The larva,

which is the true witchety grub of the Aborigines (p. 223), *Xyleutes* sp., forms a silk-lined tunnel in the soil and feeds externally on the roots of *Acacia kempeana* in

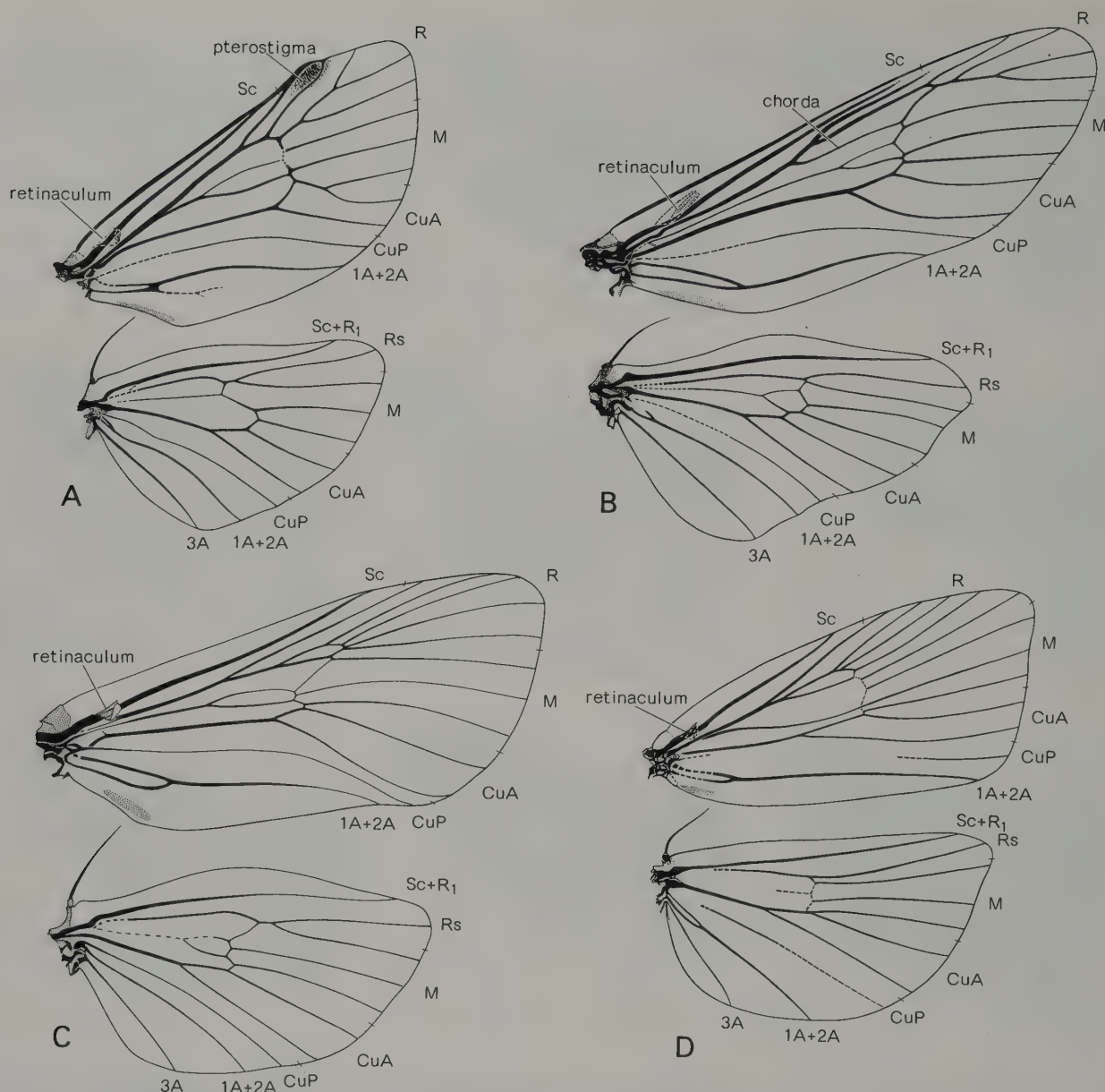


Fig. 41.48 Wing venation of Cossoidea and Tortricidae: A, *Idioses*, B, *Xyleutes*, Cossidae; C, *Dudgeonea*, Dudgeoneidae; D, *Tanychaeta*, Tortricidae.

[A, B, D by T. Binder; C by I. F. B. Common]

central Australia. The widely distributed genus *Zeuzera* (2 spp.) is restricted to northern Australia.

**41. Dudgeoneidae** (Plate 8, D). Medium sized; head with short, rough vestiture of lamellar scales, frons with tuft of forwardly directed scales; ocelli and chaetosemata absent; antennae unipectinate, rarely bipectinate, to tip in both sexes; proboscis absent; maxillary palps rudimentary; labial palps well developed, upturned; epiphysis present; spurs 0-2-4; hind tibiae with dorsal crest of long lamellar scales; fore wing (Fig. 41.48C) with retinaculum between costa and Sc; with branched M in cell and chorda,  $R_4$  to apex, CuP well developed; 1A+2A with prominent fork; hind wing with frenulum of numerous fine bristles in female, Sc+ $R_1$  and Rs subparallel, Rs and  $M_1$  stalked, CuP present distally, 2 anal veins present;

abdomen with paired, simple tympanal organs on S2 (Minet 1983); ovipositor well sclerotised, non-piercing. Larva and pupa unknown.

The family contains only the genus *Dudgeonea* (3 spp.), known from Africa, Madagascar, India, Malaysia, New Guinea and northern Australia. All species are reddish brown with circular, silvery-white spots on the fore wing. The genus has been placed in the Cossidae, Sesiioidea and Pyraloidea by various authors. The biology of *D. actinias* (Plate 8, D) was briefly described by Turner (1902); the larvae are stem-borers which excavate a tunnel to the outside bark prior to pupation and the pupae are protruded from the larval tunnel before eclosion. The only known host plant is *Canthium attenuatum*.



## Superfamily TORTRICOIDEA

**42. Tortricidae** (leafrollers) (Figs 41.47E–H). Small; head (Fig. 41.49E) vestiture usually short, rough, frons in upper half with usually long scales directed forwards, with short upwardly directed scales in lower half; ocelli usually present; chaetosemata present; antenna usually filiform; proboscis naked; maxillary palps small, 4- to 1-segmented; labial palps short to long, usually porrect, rarely upturned; epiphysis present; spurs 0-2-4; hind tibiae sometimes with modified scales; fore wing (Fig. 41.48D) often with costal fold in male, retinaculum on Sc in male, pterostigma normally absent, chorda and M-stem sometimes present in cell, CuP usually present at least distally, 1A+2A with prominent fork; hind wing broad, often with cubital pecten at base of CuA, female frenulum of 3 bristles, CuP usually present distally; abdomen unspined dorsally, S2 apodemes tortricoid, segment 8 in males sometimes with coremata, segment 7 in female sometimes with dense, deciduous scaling (corethrogyne). Eggs usually flat, scale-like, laid singly, in small groups, or in imbricate masses, sometimes covered with corethrogyne scales (Powell and Common 1985). Larva (Fig. 41.11) with prothoracic shield and pinacula often sclerotised, crochets uni-, bi- or triordinal in complete circle, an anal fork with straight prongs often present above anus; prothoracic L group trisetose, L1 and L2 adjacent on abdominal segments 1–8, often on same pinaculum; joining leaves or shoots, rarely leaf-mining (usually in early instars), or tunnelling in flower spikes, fruits, stems or galls. Pupa (Figs 41.49C, D) with 2 transverse rows of dorsal spines usually present on abdominal segments 3–7, head often with spine, posterior end usually with warts or with cremaster and hooked setae; in larval shelter, protruded at ecdysis.

The family is well represented in Australia where all three subfamilies occur, and the fauna contains several tribes regarded as primitive (Horak and Brown, in press). The large subfamily Tortricinae is most abundant in southern Australia, while the other large subfamily, the Olethreutinae, is more diverse in northern Australia. The Chlidanotinae are represented by few species.

TORTRICINAE have 2 annuli of scales per flagellar segment, usually no cubital pecten, aedeagus articulating with the juxta and the female sterigma connected to the ventral arm of the apophyses anteriores; the sex pheromones in most are 14-carbon compounds. Seven of the 10 recognised tribes of this subfamily occur in Australia. Larvae of *Phricanthes asperana* (Phricanthini) (Fig. 41.47E) feed in pod-shaped shelters on leaves of *Hibbertia scandens* in eastern Australia; the larvae lack an anal fork. *Proselena annosana* (Schoenotenini), with reduced ocelli and fore wing with raised scales, occurs in eastern Australia where the larvae feed on *Bursaria spinosa*, first in a mine, later between joined leaves. The Cochylini (formerly family Cochyliidae or Phaloniidae) are poorly represented in Australia by few species in *Clysiana*; their biology is unknown. The primarily Australian Epitymbiini have larvae feeding on dead leaves, mainly of *Eucalyptus*, thus helping to reduce the forest leaf litter to humus; *Epitymbia cosmota* (Fig.

41.47G) is a sexually dimorphic species occurring widely in eastern and south-eastern Australia (Horak and Common 1985). *Eboda exeristis* is one of the few Australian members of the Tortricini; the larvae feed on *Eucalyptus grandis*. The larvae of the largest Australian tribe, the Archipini, feed between joined, living leaves. The tribe includes many serious pests, the most important of which is the Australian light-brown apple moth, *Epiphyas postvittana*, which has become established abroad. Its larvae feed on a wide range of native and introduced plants. The large genus *Epiphyas* (40 spp.) includes several similar-looking species. Larvae of *Homona spargotis* attack avocado in northern Qld and *Merophyas divulsana*, the lucerne leaf-roller, is a pest of lucerne. *Cryptoptila* contains large species in eastern Australia and New Guinea; the larvae feed between joined leaves of many trees and shrubs, sometimes gregariously in a webbing. Larvae of *Arotrophora* (Fig. 41.47F), previously placed in the Cnephasiini, tunnel in flower spikes of *Banksia*.

CHLIDANOTINAE lack a costal fold and often have characteristic valvae and hair-pencils arising on segment 8. Chlidanotini, which typically rest with the tip of the fore wing bent upwards, are represented by 8 species in Australia (Tuck 1981). *Trymalitis optima* is a rainforest species from Qld and northern N.S.W. Polyorthini and Hilarographini are represented by 3 and 2 species respectively.

OLETHREUTINAE have one annulus of scales per flagellar segment, the fore wing has strigulae along the costa and, in the Eucosmini, often a costal fold, the aedeagus is fused with the anellus and juxta, and the sterigma is not connected to the apophyses anteriores; the sex pheromones are mainly 12-carbon compounds. This is a large subfamily with about 100 often widely distributed and mainly Oriental genera in Australia, particularly northern Australia. All of the six tribes (Horak and Brown, in press) occur in Australia.

*Gatesclarkeana tenebrosa* from northern Qld is the only named Australian species of Gatesclarkeanini; its biology is unknown. Larvae of Bactrini bore in stems of Cyperaceae and Juncaceae but little is known about the biology of the many Australian species of *Bactra*. The Microcorsini include few named species in Australia; *Cryptasasma sordida* from eastern Australia has been reared from fruits of *Acmena*. *Lobesia* and *Sorolopha* are representatives of the Olethreutini, a group particularly diverse in rainforest habitats; *Lobesia* species feed in or between webbed flowers and fruit. Eucosmini is the largest olethreutine tribe in Australia, including a typically Australian element. *Bathrotoma constrictana* has larvae which form a small, portable case of the flower buds or seed capsules of *Callistemon* and *Melaleuca* in eastern Australia. The Mexican *Epinotia lantana* was introduced to assist in the control of *Lantana*. *Crocidosema plebejana* (Fig. 41.47H) occurs widely abroad and throughout mainland Australia; its larvae feed in the seed capsules of Malvaceae and cause damage to the growing tips of cotton. *Cryptophlebia ombrodelta*, the macadamia nutborer, is also widely distributed abroad; it causes

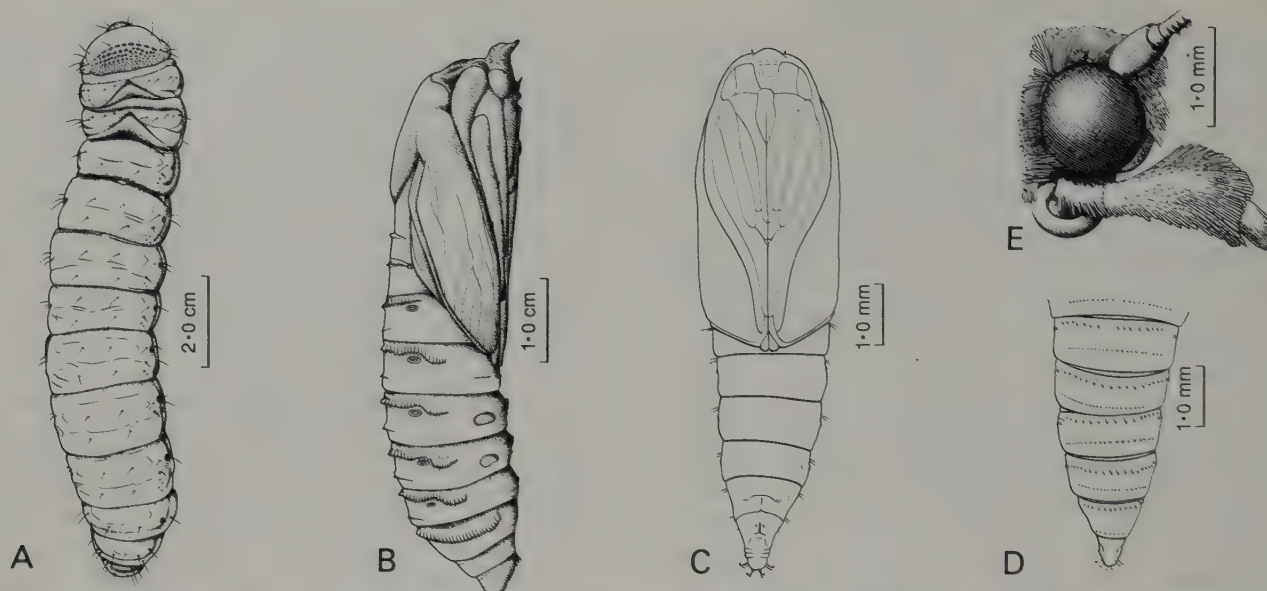


Fig. 41.49 A, B, larva and pupa of *Xyleutes*, Cossidae; C, D, pupa, ventral and dorsal, of *Epiphyas*, Tortricidae; E, head of *Epiphyas*, lateral. [J. Wedgbrow]

damage to *Macadamia* in Australia and is a member of a complex of closely related species. The Grapholitini include two important introduced pests, the codling moth *Cydia pomonella* and the oriental fruit moth, *Grapholita molesta*, which attack pome and stone fruit respectively. The large fauna of native species contains many metallic coloured and possibly day-flying species with larvae which are internal feeders in fruits and pods or, as in *Cydia metallicosma*, bore in stems of mistletoe. [Common 1965b; Horak 1984]

### Superfamily CASTNIOIDEA

**43. Castniidae** (Plate 8, B; Fig. 41.471). Medium sized; head smooth scaled, vertex with lamellar scales directed forwards, frons with piliform scales; ocelli present, large; chaetosemata absent; antennae with smooth-scaled flagellum, broadly clubbed apically; proboscis present or reduced, naked; maxillary palps small, 2–4-segmented; labial palps short, ascending; epiphysis slender, spine-like; spurs 0–2–4; legs smooth scaled; fore wing (Fig. 41.50A) broad, M present in cell, chorda present or absent,  $M_1-M_2$  cross-vein weak, CuP present or absent,  $1A+2A$  with long fork; hind wing with frenulum of 3 fine bristles in female, M present in cell, Sc+ $R_1$  separate from or shortly fused with Rs near base,  $M_1-M_2$  cross-vein absent (cell 'open'), CuP present or absent; ovipositor long and telescopic. Eggs flat, fusiform, with prominent ridges. Early-instar larva with well sclerotised prothoracic shield, L1 and L2 approximate on one pinaculum on abdominal segments 1–8; ventral prolegs with 2 transverse rows of uniordinal crochets; mature larva of *Synemon* cossid-like, without prolegs and crochets and with a few secondary setae; tunnelling in monocotyledons or in silk-lined, adjacent tunnels in soil. Pupa (Fig. 41.60A) with antennae swollen at apex, abdominal terga with 2 transverse rows of spines on T2–7 in males and

T2–6 in females, and 1 row on T7 in females and T8 and 9 in both sexes. Spiracles large; cremaster absent; pupa in silk-lined tunnel or cocoon in larval gallery, protruded at ecdysis.

Because of their clubbed antennae and day-flying habit, earlier authors often thought the castniids were closely related to the butterflies, a view that can no longer be upheld. All the Australian species belong to the endemic genus, *Synemon*, which has been placed in its own subfamily by early workers; this needs reassessment.

*Synemon* (Fig. 41.471) (34 spp.) occurs widely in mainland Australia and reaches maximum diversity in southern W.A. The adults fly rapidly, close to the ground on sunny days. The hind wings of most species are brightly coloured while the fore wings are cryptically patterned. The larvae of *S. magnifica* (Plate 8, B) feed on *Lepidosperma viscidum*; they first tunnel in the butt of the host below ground level and later construct a vertical tunnel, projecting above the soil at the base of the host plant, in which pupation takes place (Common and Edwards 1981). Other species are known to feed on *Danthonia laevis* and *Lepidosperma carphoides*. The life cycle takes 2 to 3 years.

### Superfamily SESIOIDEA

Small to medium sized; head usually smooth; ocelli usually present; chaetosemata present or absent; proboscis naked or scaled at base; fore wing with M sometimes retained in cell, chorda sometimes present, CuP usually weak or absent; wing coupling sometimes specialised; abdomen without dorsal spines, S2 of tortricoid type. Larva usually with 3 L setae on prothorax. Pupa with abdominal segments 3–7 movable in male, 3–6 in female and segments 2–7 with 1 or 2 dorsal transverse rows of spines; cremaster absent, but often with posterior hooked setae; pupae protruded at ecdysis.

The three families Brachodidae, Sesiidae and Choreut-



idae, placed in the Sesiioidea (Heppner and Duckworth 1981), are not known to share any synapomorphies and

the grouping seems to be based largely on the similarity of the immature stages.

*Key to the Families of Sesiioidea Known in Australia*

1. Proboscis scaled at base ..... **Choreutidae** (p. 877)
- Proboscis naked ..... 2
- 2(1). Fore wing greatly narrowed, wing coupling specialised, wings partially hyaline ..... **Sesiidae** (p. 876)
- Fore wing not unusually narrowed, wing coupling normal, wings not hyaline ..... **Brachodidae** (p. 875)

**44. Brachodidae** (Atychidae) (Fig. 41.47j). Small; head with loosely appressed slender or broad lamellar scales; ocelli large; chaetosemata absent; antennae uni- or bipectinate, lamellate or thickened with scales in male, filiform in female; proboscis unscaled; maxillary palps minute, 1-3-segmented; labial palps short, slightly recurved; epiphysis present; spurs 0-2-4; fore wing (Fig. 41.50b) without pterostigma, retinaculum on spur of Sc, chorda often present, M vestigial in cell,  $R_4$  to costa near apex, CuP present at margin or vestigial, 1A+2A with prominent fork, hind wing with frenulum of 2 bristles in female, Sc+ $R_1$  strong and diverging from Rs from base,

$M_3$  often stalked with CuA $_1$ ; abdomen often long, ovipositor extensible. Larva with weakly sclerotised prothoracic shield, 2 L setae on prothorax, ventral prolegs with crochets in 2 uniordinal, transverse rows; borers. Pupa with projection on head; T2-7 in male and T2-6 in female each with 2 transverse rows of spines.

The adults of many Australian species have yellow or pale hind wings and cryptically coloured fore wings. Although the family is widely distributed in eastern, southern and western Australia, these day-flying moths, which occur mainly in dry areas, are little known. The endemic genus *Miscera* (20 spp.) includes the brightly

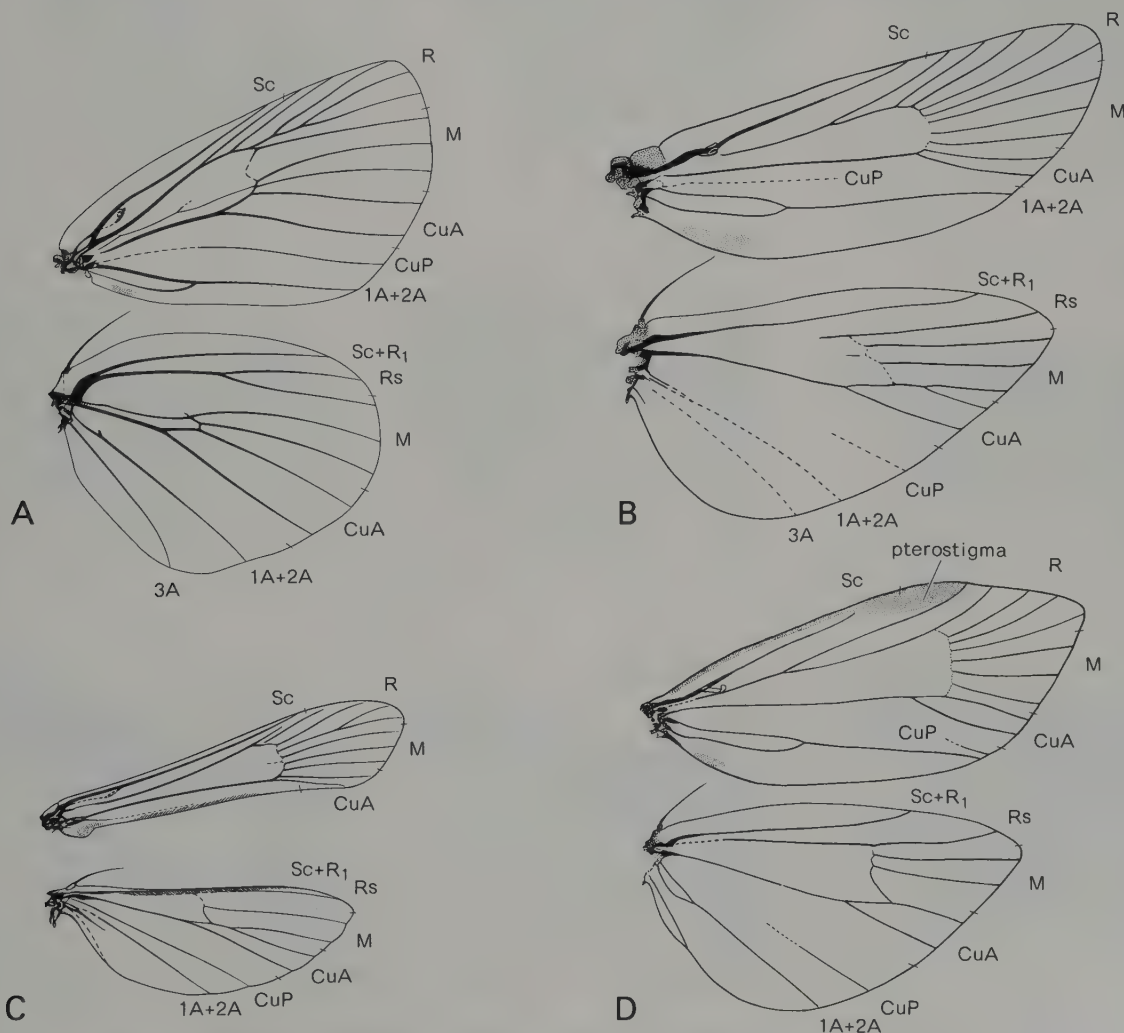


Fig. 41.50 Wing venation of Castnioidea and Sesiioidea: A, *Synemon*, Castniidae; B, *Miscera*, Brachodidae; C, *Synanthedon*, Sesiidae; D, *Tebenna*, Choreutidae. [A, C by J. Wedgbrow; B, D by I. F. B. Common]

coloured *M. androgyna*, but most species have greyish fore wings. The small genera *Synechodes* and *Euthoribeta* are also endemic. *Nigilgia adjunctella* (Fig. 41.47j), which also occurs in Africa and Asia, is locally common in northern Qld where it is associated with the introduced ornamental *Tamarindus indica*.

**45. Sesiidae** (Plate 7, D). Small to medium sized; head smooth scaled, with piliform scales on vertex, lamellar scales on frons; ocelli present, large; chaetosemata present, small; antenna often thickened, rarely pectinate, usually clavate with apical tuft, or filiform with long ventral cilia; proboscis usually well developed, unscaled; maxillary palps small, 1–3-segmented; labial palps recurved, sometimes tufted; epiphysis present; spurs 0–2–4; hind tib-

iae sometimes with prominent tufts or scaling; fore wing (Fig. 41.50c) long and narrow, without pterostigma, dorsum forming longitudinal downward fold fitting around upward costal fold of hind wing, wing usually partially hyaline,  $R_4$  and  $R_5$  stalked, CuP absent,  $1A+2A$  short, unforked; hind wing with frenulum of one bristle in both sexes,  $Sc+R_1$ ,  $Rs$  and costa closely approximated, CuP often present. Abdomen often brightly coloured, uncus and valvae usually with dense setae. Larva pale, 3 L setae on prothorax, crochets in 2 uniordinal transverse rows; tunnelling in trunk, bark or roots of trees and herbs, or in galls. Pupa with projections on head, T2–7 in males and T2–6 in females each with 2 transverse rows of spines, T8 in male and T7 and 8 in female each with one row; anal



Fig. 41.51 A, *Lactura suffusa*, Zygaenidae; B, *Doratifera vulnerans*, Limacodidae; C, *Heteropsyche melanochroma*, Epipyropidae; D, *Cyclotorna monocentra*, Cyclotornidae; E, *Imma vaticina*, F, *Imma acosma*, Immidae; G, *Phycomorpha prasinochroa*, Copromorphidae; H, *Carposina neurophorella*, I, *Bondia nigella*, Carposinidae. Scales = 2 mm.

[C. Lourandos, E. Slater]



setae present, cremaster absent, segments 3–7 in male and 3–6 in female movable, partly protruded at ecdysis.

Only 14 named species of this rather large family occur in Australia (Duckworth and Eichlin 1974). The diurnal, often brightly coloured moths bear a remarkable resemblance to wasps and bees. Their flight is rapid and they often visit flowers. The tinthiine *Pennisetia igniflua* from the Brisbane (Qld) area has larvae that tunnel in the trunk of the rainforest tree *Elaeocarpus grandis*. The sexually dimorphic and larger *Albuna oberthuri* occurs in the N.T. *Carmenta chrysophanes* (Plate 7, D) is widely distributed in eastern Australia; the larvae are known from several hosts including the woody galls on the branches of *Exocarpos cupressiformis*. The larvae of the introduced currant borer moth, *Synanthedon tipuliformis*, tunnel in the stems of currants and gooseberries in N.S.W., Vic. and Tas.

**46. Choreutidae** (Figs 41.47K, L). Very small to small; head smooth scaled; ocelli large, chaetosemata absent; antennae filiform, sometimes thickened by dorsal scaling, cilia often long; proboscis scaled at base; maxillary palps minute, 1- or 2-segmented; labial palps recurved, 2nd segments often tufted ventrally; epiphysis present; spurs 0-2-4; fore wing (Fig. 41.50b) broadly triangular, pterostigma present, hind wing with usually 3 frenular bristles in female, Sc+R<sub>1</sub> and Rs diverge from base, M<sub>3</sub> and CuA<sub>1</sub> often stalked; abdomen without coremata. Larva with 6th stemma often reduced, prothoracic shield and pinacula well sclerotised, L group trisetose on prothorax; crochets uniordinal in complete circle, rarely biordinal or in lateral penellipse; feeding externally or beneath flimsy web. Pupa (Fig. 41.60b) with slightly fused appendages, T2–7 each with one transverse row of spines, cremaster absent,

hooked anal setae sometimes present; pupation in silk cocoon, pupa protruded at ecdysis.

The adults (Figs 41.47K, L), often with metallic patterns, are diurnal, flying in sunshine or sitting on flowers. They walk in a characteristic, jerky manner and, at rest, often curl their wings. *Tebenna micalis* is a widely distributed species with larvae feeding on Asteraceae, including *Helichrysum* and introduced thistles. The green larvae live in a web beneath the leaves and pupate in a silk cocoon in the web. The larvae of *Choreutis basalis* form a silk shelter on leaves of *Ficus*. *Saptha* (8 spp.) contains relatively large and brilliantly coloured species; *S. exanthista* is from rainforest in northern Qld. [Arita 1987; Heppner and Duckworth 1981; Diakonoff 1986]

### Superfamily ZYGAENOIDEA

Small to large; ocelli and chaetosemata present or absent; M often present in cell, CuP usually present, hind wing with Sc+R<sub>1</sub> not approximate to Rs beyond cell. Larva stout, sluggish, feeding exposed or ectoparasitic on plant-hoppers or in ant nests. Pupa relatively broad and short, with dorsal spines, and spiracles of 1st abdominal segment visible (except in Epipyropidae); protruded at ecdysis. The tendency for the veins Sc and Rs of the hind wing to fuse, the slug-like larvae and the pupae usually with an exposed 1st abdominal spiracle, are probably the best characters to support the monophyly of this superfamily. Subgroups share such obvious specialisations as larval heteromorphosis in Cyclotornidae, Limacodidae and Epipyropidae, parasitic larvae in Epipyropidae and Cyclotornidae, and the loss of the proboscis in all families except Zygaenidae.

### Key to the Families of Zygaenoidea Known in Australia

- |       |  |                               |
|-------|--|-------------------------------|
| 1.    | Proboscis well developed .....   | <b>Zygaenidae</b> (p. 877)    |
|       | Proboscis vestigial or absent .....  | 2                             |
| 2(1). | Fore wing with R <sub>3</sub> , R <sub>4</sub> and R <sub>5</sub> stalked .....                                  | <b>Limacodidae</b> (p. 878)   |
|       | Fore wing with all veins arising separately from end of cell, or R <sub>4</sub> and R <sub>5</sub> stalked ..... | 3                             |
| 3(2). | Tibial spurs 0-2-4 .....   | <b>Cyclotornidae</b> (p. 879) |
|       | Tibial spurs absent .....  | <b>Epipyropidae</b> (p. 879)  |

**47. Zygaenidae** (burnets, foresters) (Plate 6, ZC; 7, N; Fig. 41.51A). Small; head smooth scaled; ocelli present or absent; chaetosemata present (absent in the African subfamily Charideinae), often large; antennae filiform, serrate, bipectinate or clubbed, often thick; proboscis well developed in Australian taxa, unscaled; maxillary palps small, 1- or 2-segmented; labial palps ascending, short; epiphysis present or absent; spurs 0-2-4, 0-2-2 or absent; hind tibiae smooth; wings (Fig. 41.52A) rounded, often broad, CuP absent and chorda present in *Lactura* group, 1A+2A with short fork; hind wing with 1–3 frenular bristles in female of Australian species, Rs sometimes reduced basally, Sc+R<sub>1</sub> close to or fused with Rs at base or at midlength, CuP present; apophyses in ovipositor small and slender in Australian species. Larva short and broad, with secondary setae on verrucae and lateral, gland-like structure on segments 2 and 7 in Zygaeninae and Procrinae, crochets in uniordinal mesoserries, anal

fork sometimes present. *Lactura* group larvae slug-like, with eversible lateral lobes, prothorax with trisetose L group, crochets in a biordinal, mesal penellipse. Larvae feed exposed. Pupa (Fig. 41.60c) stout and flattened, abdominal T2–8 or T3–8 each with transverse row of spines; with a few hooked anal setae; cremaster absent; protruded at ecdysis through broad, horizontal 'frog-mouth' slit in elongate or broadly oval, slightly domed cocoon.

Many zygaenid adults fly and feed at flowers during the day. *Thyrassia inconcinna*, without spurs, from northern Qld, resembles a small ctenuchine arctiid; larvae of *Thyrassia* feed on *Vitis*. *Pollanisus* (12 spp.; Plate 7, N) with brilliant coppery or metallic blue scales, is the largest genus in Australia; the larvae of *P. viridipulverulenta* feed in late winter on flower-buds and leaves of *Hibbertia*. The wasp-like *Hestiochora tricolor* (Plate 6, ZC) has larvae feeding on *Eucalyptus* and *Syncarpia*. The





spurs, is widely distributed in Australia; the brightly coloured larvae feed exposed on foliage of *Eucalyptus* and other Myrtaceae and have paired dorsal protuberances which are crowned with eversible tufts of stinging hairs; the larvae of *D. oxleyi* often seriously defoliate *Eucalyptus*, and the larvae of *D. vulnerans* (Fig. 41.51B) which also feed on *Eucalyptus*, are known to defoliate apricot trees. *Doratifera* larvae pupate in a pyriform cocoon attached to twigs or bark. *Comana* (12 spp.) (Plate 7, J) occurs mainly in northern Australia. *Mecytha fasciata* is a handsome species from northern and eastern Australia with a relatively smooth larva which lacks prominent tubercles and stinging hairs; its food plants all belong to the Proteaceae. Larvae of *Scopelodes*, with two species in northern Qld, have stinging hairs.

**49. Epipyropidae** (Fig. 41.51C). Very small; head with appressed lamellar scales; antennae short, bipectinate to apex in both sexes; ocelli, chaetosemata, proboscis and maxillary palps absent; labial palps minute, drooping; epiphysis and tibial spurs absent; wings (Fig. 41.52C) broad; fore wing without retinaculum, all veins arising separately from discal cell, M present or vestigial in cell, chorda present, CuP present near margin; hind wing with 1 frenular bristle in both sexes, Sc+R<sub>1</sub> well separated from Rs, R<sub>1</sub> sometimes present, CuP and 1 or 2 anal veins present. Eggs disc-like or ovate. Larva heteromorphic; 'sub-campodeiform' at first, with large head and thorax; later strongly convex, covered with white waxy secretion, crochets uniordinal in a circle, antennae long, ocelli closely grouped, mandibles long, pointed, minutely dentate apically; in Australia ectoparasitic upon planthoppers (Fulgoroidea, HEMI). Pupa (Fig. 41.60D) in white, oval or rosette-shaped cocoon (Fig. 41.53b) with horizontal 'frog-mouth' slit through which pupa protrudes at ecdysis.

The adults, which are all dark grey, fly at dusk and are attracted to light. The eggs are laid singly or in clusters on the food plants of the planthopper hosts. The 1st instar larvae seek actively for a host, and often adopt an erect questing posture as they await its approach. After the first ecdysis they are incapable of parasitising a second host, should they be dislodged. The feeding habits of the larva have not been determined precisely, but the larva probably ruptures the cuticle of its host with its mandibles and feeds on the haemolymph; in some species the host succumbs. In northern and eastern Australia the hosts of *Heteropsyche* (7 spp.) include *Platybrachys* spp. on *Eucalyptus* and *Scolypopa australis* on passion vines. *H. melanochroma* (Fig. 41.51C) is one of several similar species. [Krampl and Dlabola 1983]

**50. Cyclotornidae** (Fig. 41.51D). Small; head with appressed lamellar scales and 2 whorls of raised piliform scales; ocelli and chaetosemata absent; antennae simple, thickened, scape with pecten; proboscis and maxillary palps absent; labial palps very short; epiphysis absent, tibial spurs 0-2-4, hind tibiae with long hair-scales; fore wing (Fig. 41.52B) with chorda present, M forked in discal cell, R<sub>4</sub> and R<sub>5</sub> stalked or separate, R<sub>5</sub> to apex, other veins separate, CuP present, 2A running separately towards margin from fork of 1A+2A; hind wing with M

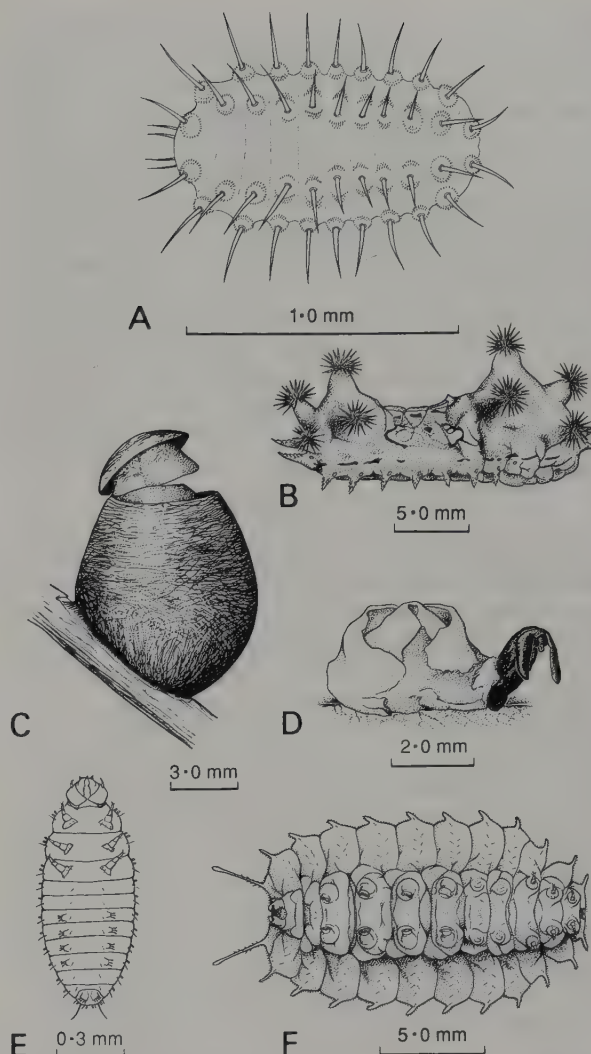


Fig. 41.53 Larvae and cocoons of Zygaenoidea: A, 1st instar larva of *Pseudanapaea*, Limacodidae; B, C, larva and cocoon of *Doratifera*, Limacodidae; D, cocoon of *Heteropsyche*, Epipyropidae; E, F, 1st and final instar larvae of *Cyclotorna*, Cyclotornidae.

[A by I. F. B. Common; B-F by S. Monteith]

simple in cell, Sc+R<sub>1</sub> strong, CuP present, 2A running separately towards margin from fork of 1A+2A. Abdomen stout. Eggs oval, flattened. Larva heteromorphic, 1st instar (Fig. 41.53E) flattened, with large head and long, pointed mandibles, mature larva (Fig. 41.53F) with small head, long antennae, apical adhesive pads on thoracic legs, crochets in uniordinal mesoserries, and fine secondary setae; at first parasitic on leafhoppers (Eurymelidae), later predatory on ant larvae. Pupa dorso-ventrally flattened, in oval, white, silken cocoon with horizontal 'frog-mouth' slit through which the pupa protrudes at ecdysis.

Endemic to Australia, the stout-bodied moths may be recognised by the condition of the A veins in both wings. Most are grey, some with distinct dark spots on the fore wing; a few are yellowish white and at least one species is yellow and black. The adults come to light. As in Epipyropidae, the females lay a large number of eggs.



The remarkable life history of *Cyclotorna monocentra* (Fig. 41.51D) was described by Dodd (1912). The eggs are laid on the twigs and bark of a tree already infested with Eurymelidae, which are usually attended by ants. The flat, 1st instar larva (Fig. 41.53E) is an external parasite of a leafhopper. It later spins an oval, flat shelter beneath bark, in which it moults to a brightly coloured, flattened larva with retractile head and body segments laterally expanded. This is carried by an ant to its nest, where the moth larva feeds upon the ant larvae, yielding an anal secretion eagerly devoured by the ants. At maturity, the larva (Fig. 41.53F) spins its cocoon beneath loose bark on a nearby tree. In the smaller *C. egena*, lacking CuA<sub>1</sub> in the hind wing, the first-stage larvae parasitise Psyllidae. In some species early ecdyses occur in silk shelters spun on the body of the leafhopper host.

### Superfamily IMMOIDEA

**51. Immidae** (Figs 41.51E, F). Small; head smooth, with lamellar scales; ocelli usually absent, chaetosemata usually present; antennae filiform; proboscis well developed, unscaled; maxillary palps minute, 1- or 2-segmented; labial palps curved upwards, 2nd segment with dense scales, apical segment slender and pointed; epiphysis present; spurs 0-2-4; hind tibiae smooth scaled; fore wing (Fig. 41.55A) with male retinaculum on Sc, chorda and stem of M absent in cell, R<sub>4</sub> and R<sub>5</sub> sometimes stalked, R<sub>5</sub> and sometimes R<sub>4</sub> to termen, CuP present near margin, 1A+2A fork prominent; hind wing sometimes partly transparent, female frenulum of 3 bristles, vestigial M-stem present in cell, Rs and M<sub>1</sub> usually stalked, CuP present near margin, 3A present; abdomen sometimes with coremata. Larva slender, without secondary setae, more dorsal setae barbed, prothorax with 3 L setae on one pinaculum; ventral prolegs slender with crochets in unior-

dinal mesoseries; feeding exposed. Pupa (Fig. 41.60E) slightly compressed, lightly sclerotised, abdominal terga without spines, segments 5 and 6 movable; without cremaster but with about 16 hooked setae; cocoon of white silk, pupa not protruded at ecdysis.

The adults (Figs 41.51E, F) are relatively stout bodied and nocturnal. *Imma acosma* (Fig. 41.51F) is the best known Australian species (Common 1979); it occurs in eastern Qld and N.S.W.; the green larva feeds fully exposed on the foliage of *Hymenanthera dentata* and pupates in a white, silk cocoon beneath a network of silk stretched across a slight hollow. *I. lyrifera* from northern Qld has partly transparent hind wings and *I. stilbiota* is a large, noctuid-like species from Qld and the Torres Strait islands. At least one unnamed species is known from north-western W.A. The black and orange *Birthantha cleis*, the most conspicuous Australian species, occurs in the N.T. and northern Qld.

### Superfamily COPROMORPHOIDEA

Small; head smooth scaled; ocelli present or absent; chaetosemata absent; scape without pecten; proboscis naked; maxillary palps small; labial palps usually prominent, recurved or porrect; fore wing often with raised scale-tufts, CuA of hind wing often with pecten; spurs 0-2-4. Larva with 2 L setae on prothorax, crochets uniordinal, usually in circle; tunnelling in flowers, bark, fruits and galls, sometimes between joined leaves. Pupa without dorsal spines, segments 5-7 movable in male, 5-6 in female, tip with group of hooked setae; not protruded at ecdysis.

The 2 families here included in the Copromorphoidea are very similar but evidence of monophyly is sparse (Minet 1986). The most significant character is the long, curved, anterolateral processes on S2. [Kyrki 1983a]

#### Key to the Families of Copromorphoidea

- Hind wing with 3 branches of M present ..... **Copromorphidae** (p. 880)  
Hind wing with 1, or more usually 2, branches of M absent ..... **Carposinidae** (p. 880)

**52. Copromorphidae** (Fig. 41.51G). Small; head (Fig. 41.54A) smooth scaled, scales long and slender; ocelli present or absent; antennae simple, unipectinate or rarely bipectinate; maxillary palps small, 1- or 4-segmented; labial palps prominent and upturned or long and porrect; epiphysis present; hind tibiae usually with long hair-scales above, sometimes (*Osidryas*) with dorsal hair-pencil; fore wing (Fig. 41.55B) usually with raised scale-tufts, vestigial chorda and M-stem sometimes present in cell, R<sub>5</sub> to termen, M<sub>3</sub> and CuA<sub>1</sub> approximated at base, CuP vestigial or present near margin, 1A+2A fork short; hind wing broader than fore wing, female with 2 or 3 frenalur bristles, Rs and M<sub>1</sub> parallel, CuA usually with pecten, CuP present. Larva stout with short ventral prolegs and uniordinal crochets in complete circle or sometimes biserial inner crochets; spiracles slightly protruding, those on segment 8 more dorsal; tunnels in leaf veins, twigs and fruit or between joined leaves. Pupa in larval gallery or silk-lined cell.

A small, mainly Asian-Australian family. The adults of

*Copromorpha* (8 spp.) and *Phycomorpha* (1 sp.) rest with the wings folded flat above the abdomen and have tufts on the fore wing. *P. prasinochroa* (Fig. 41.51G) is rich green and occurs in rainforests in eastern Qld and N.S.W.; the white larva bores in stems, twigs and fruits of cultivated or native figs or feeds between leaves of *Ficus coronata*; it pupates in a silk-lined cell. The larger *C. lichenitis* is known from rainforest in southern Qld and northern N.S.W. *Osidryas* (2 spp.), which occurs in rainforests in eastern Qld and north-eastern N.S.W. has long, porrect palps, and lacks scale-tufts and a cubital pecten.

**53. Carposinidae** (Figs 41.51H, I). Small; head (Fig. 41.54B) with frons smooth scaled, vertex with lateral tufts; ocelli rarely present; antennae to three-quarter length of fore wing, filiform, with dense cilia in male; maxillary palps minute, 1-segmented; labial palps prominent, in male slightly upcurved with porrect apical segment, in female longer and porrect, 2nd segment in both expanded with scales; epiphysis present; hind tibiae with long hair-scales above; fore wing (Fig. 41.55C) some-



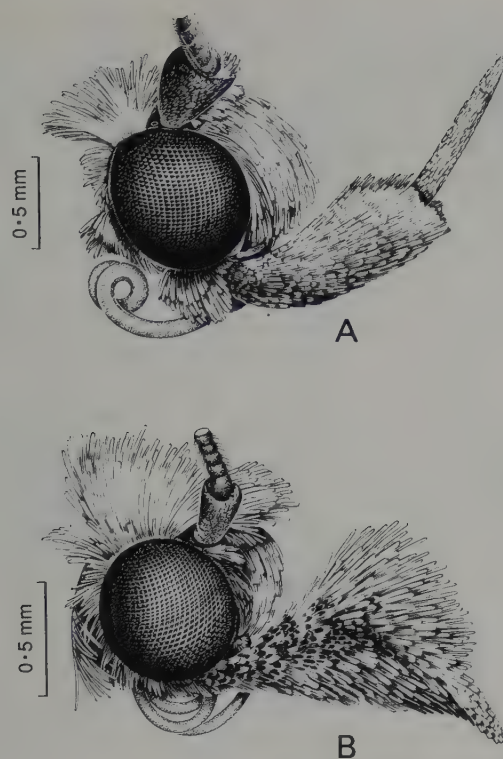


Fig. 41.54 Heads, lateral, of Copromorphoidea: A, *Phycomorpha*, Copromorphidae; B, *Carposina*, Carposinidae. [F. Nanninga]

times with pterostigma, usually with raised scale-tufts and row of short setae along dorsum, male retinaculum on Sc, chorda and M-stem absent,  $R_5$  to termen, CuP absent, 1A+2A fork small; hind wing broader than fore wing, with 2 frenular bristles in female, CuA usually with pecten and males often with specialised scales at base, M-stem absent from cell, Sc+ $R_1$  close to Rs to near end of cell,  $M_2$  and usually  $M_1$  absent, CuP present; abdomen

often with paired coremata. Larva with short ventral prolegs, crochets in uniordinal circle sometimes with lateral gap; prothorax with the two L setae on one pinaculum; spiracles on segment 8 more dorsal; tunnels in living bark, fruit or galls. Pupa (Fig. 41.60F) in larval gallery or in cocoon in soil or crevice.

The family occurs world-wide with the largest number of species in the Pacific region and Asia-Australia. Within Australia most species occur in sclerophyll forests of the south; a few are minor pests. *Bondia* (Fig. 41.51i) (6 spp.) has black fore wings and the species are well camouflaged when resting on fire-blackened trunks; larvae tunnel in necrotic bark of *Eucalyptus* just above the entrance to tunnels made by larvae of *Aenetus* (Hepialidae). *Paramorpha* (9 spp.) has pale grey fore wings with delicate markings; *P. rhachias* has been reared from flowers of *Leucopogon attenuatus*. Larvae of *Carposina autologa* feed in the woody seed capsules of *Hakea* and *C. hyperlopha*, the largest Australian species, has been reared from flower spikes of *Banksia*. The larvae of *Coscinoptycha improbana* bore in the fruits of native and introduced plants, including guava and *Citrus*.

#### Superfamily EPERMENIOIDEA

**54. Epermeniidae** (Fig. 41.56A). Very small; head smooth scaled; ocelli and chaetosemata absent; antennae with pecten; proboscis naked, small; maxillary palps small, 3-segmented; labial palps upturned, often rough scaled; epiphysis present; spurs 0-2-4; mid and hind tarsi with apical whorls of bristles, hind tibiae with prominent stiff bristles; fore wing (Fig. 41.55D) narrow, with projecting tufts of broad scales from dorsum, chorda present or absent, M-stem absent from cell,  $R_5$  to termen, CuP tubular at margin, 1A+2A with basal fork; hind wing narrower than fore wing, with 2 frenular bristles in female, M absent from cell, one short A vein present; S2 with

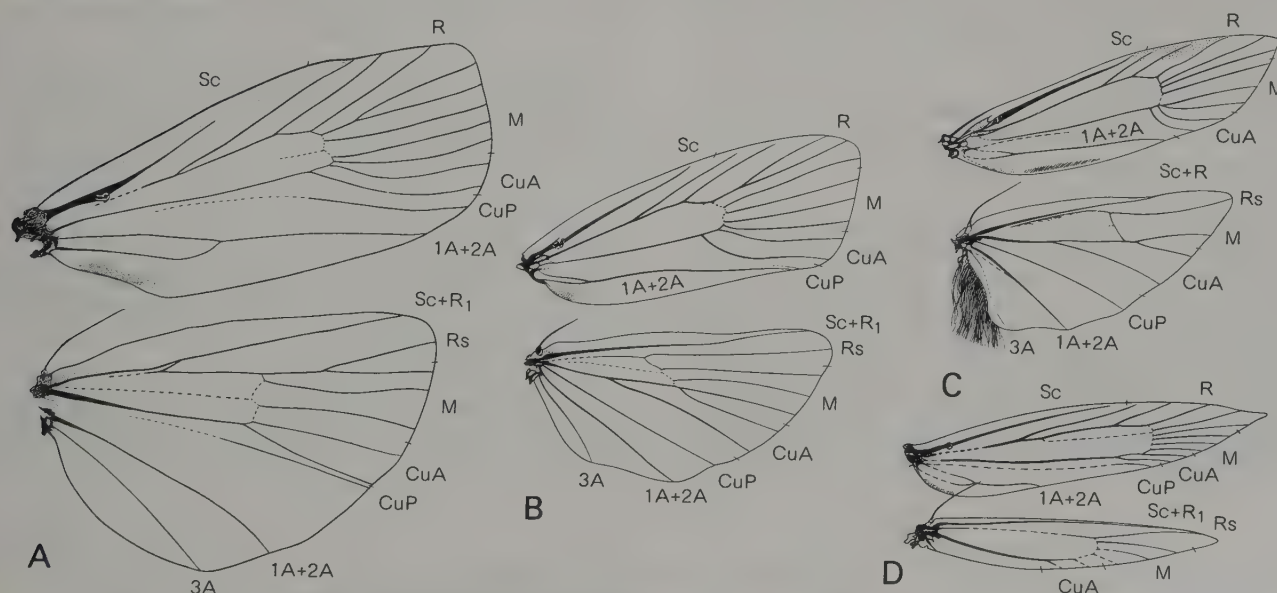


Fig. 41.55 Wing venation of Immoidea, Copromorphoidea and Epermeniioidea: A, *Imma*, Immidae; B, *Copromorpha*, Copromorphidae; C, *Carposina*, Carposinidae; D, *Epermenia*, Epermeniidae. [A by I. F. B. Common; B-D by J. Wedgberg]

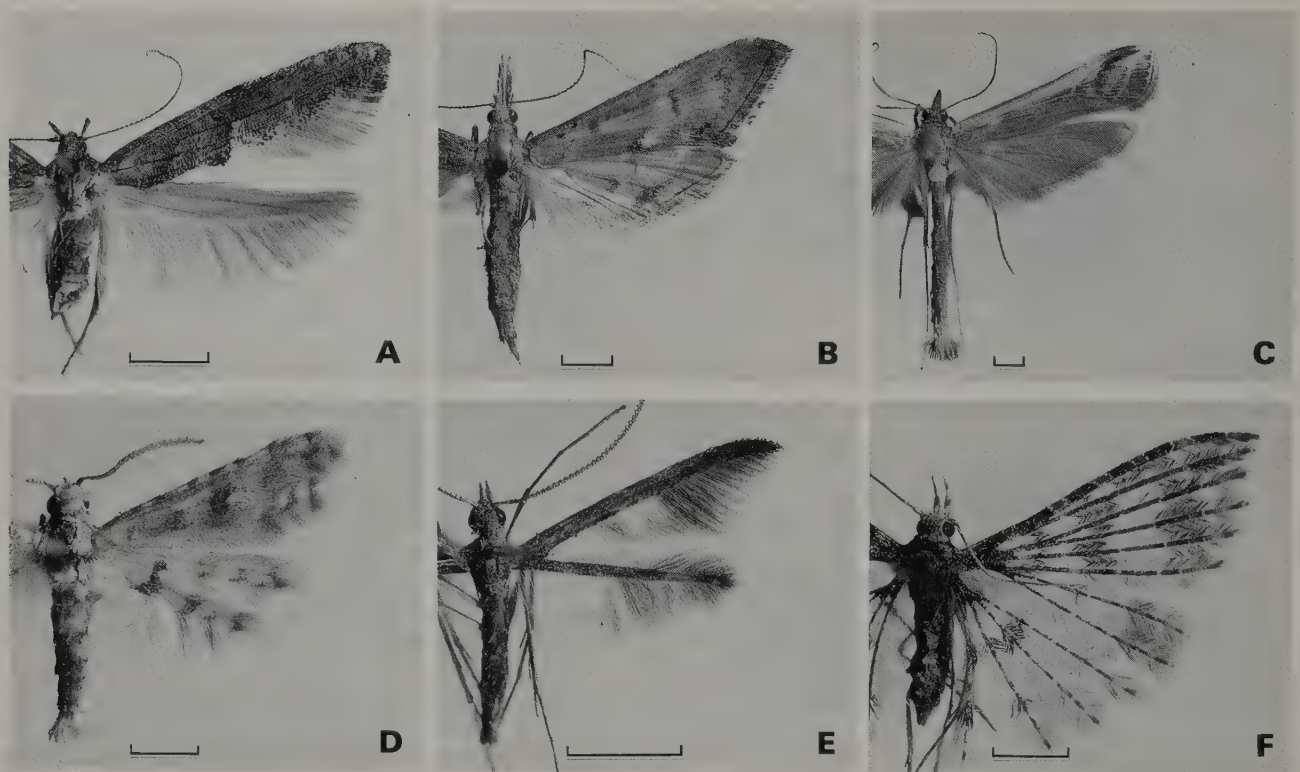


Fig. 41.56 A, *Gnathifera eurybias*, Epermeniidae; B, *Tineodes adactylalis*, C, *Tanycnema anomala*, D, *Cenoloba oblitalis*, E, *Oxychirotia paradoxa*, Tineodidae; F, *Alucita phricodes*, Alucitidae. Scales = 2 mm. [C. Lourandos]

vestigial apodemes, segment 2 with or without pleural, eversible, ciliate process; gnathos often spined medially. Egg of flat type, ovoid, laid singly. Larva with abdominal spiracle 8 largest and more dorsal, crochets uniordinal in complete circle; prothorax with 2 L setae, L1 and L2 approximate, on thorax on one pinaculum, on abdomen on separate pinacula; mines in leaves, or feeds in seeds, fruits and flowers, or under slight web, or fully exposed. Pupa (Fig. 41.60G) with very narrow prothorax, abdominal terga without spines, spiracles slightly produced, a pair of deep lateral pits on abdominal segment 9, and a small cremaster with hooked setae; in cocoon, not protruded at ecdysis.

This small family occurs world-wide and both subfamilies, OCHROMOLOPINAE and EPERMENIINAE, are represented in Australia with a total of 18 named species (Gaedike 1968, 1972, 1979). *Gnathifera eurybias* (Fig. 41.56A) is known from Qld to Tas. and S.A.; the green larvae feed exposed on *Exocarpos cupressiformis*. *Gnathifera* (11 spp.) is the largest Australian genus. The single Australian species of *Ochromolopis*, *O. cornutifera*, is known only from Mt Wilson, N.S.W. The larvae of

*Paraepermenia santaliella* feed in the fruits of quandong (*Santalum acuminatum*) in the drier areas of southern Australia. *Epermenia exilis*, one of 4 Australian *Epermenia* species, has larvae which feed within the seed capsules of *Bursaria spinosa*. [Dugdale 1988a]

#### Superfamily ALUCITOIDEA

Small, head smooth scaled, ocelli present or absent; chaetosemata absent; scape without pecten; proboscis unscaled; epiphysis present; spurs 0-2-4 or 0-0-2; wings often divided into plumes, CuP absent in fore wing; tympanal organs absent; S2 with V-shaped sclerotisation, T3-6, and sometimes T2-7 with anterior, transverse, sclerotised band set with spines. Larva densely spinulose, without secondary setae, L group on prothorax bisetose on one pinaculum, ventral prolegs with uniordinal crochets. Pupa without dorsal abdominal spines, in cocoon, not protruded at ecdysis.

The shape of the sclerotised structure on S2 and the discrete, transverse bands of spines on the abdomen of the adult provide evidence for the monophyly of this superfamily.

#### Key to the Families of Alucitoidea

- Fore wing divided into 6 plumes, hind wing divided into 6 or 7 plumes ..... **Alucitidae** (p. 883)  
 Fore wing and hind wing entire or divided into 2 plumes ..... **Tineodidae** (p. 883)



**55. Tineodidae** (including Oxychirotidae) (Figs 41.56B–E). Small; head smooth scaled; antennae filiform, from two-thirds length of fore wing to longer than fore wing; proboscis well developed; maxillary palps small, 4-segmented; labial palps moderately long, porrect; spurs 0-2-4, rarely 0-0-2; legs long and slender, hind tibiae usually smooth; fore wing (Figs 41.57A–C) narrow, triangular or deeply cleft, without wing-locking microtrichia, chorda absent and M vestigial in cell, R with branches separate or stalked, sometimes one branch missing, CuP absent, 1A+2A with small fork or vestigial; hind wing sometimes deeply cleft, with 1–3 frenular bristles, Sc often fused briefly with Rs beyond cell, CuP absent, one or more A veins sometimes absent; abdomen long and slender, T3–6 or rarely T2–7 with narrow anterior band of spines. Larva with ventral prolegs fairly long, slender, crochets uniordinal in mesal penellipse; L1 and L2 approximate on abdominal segments 1–8, on 1 pinaculum; between joined leaves or burrowing in fruits and seeds. Pupa (Fig. 41.60H) with large pilifers, without cremaster but with terminal hooked setae.

The family is restricted to Asia, New Guinea and Australia. Most species occur in Australia, where there are 10 named species in 8 named genera. *Tineodes adactylalis* (Fig. 41.56B), with ocelli and long labial palps, occurs widely, but the biology is unknown. Larvae of *Palaeodes samealis* from the north-east feed between joined leaves of *Jasminum volubile*, and those of *Euthrausta oxyprora* between leaves of *Glochidion ferdinandi*. *Cenoloba oblitalis* (Fig. 41.56D) has a deep terminal cleft in each wing; the larvae tunnel in the developing cotyledons of the large seeds of the mangrove *Avicennia marina*. The early stages of *Oxychirota paradoxa* (Fig. 41.56E), which has almost linear wings, are not known. *Tanycnema anomala* (Fig. 41.56C), from N.S.W. and Qld, superficially resembles an agdistine pterophorid.

**56. Alucitidae** (Fig. 41.56F). Small to very small; head smooth scaled with lateral tufts; antennae filiform, about half length of fore wing; proboscis present; maxillary palps small, 3–5-segmented, or absent; labial palps moderate to long, recurved, 2nd segment usually with projecting scales; spurs 0-2-4; hind tibiae with stiff, spine-like scales above; fore wing (Fig. 41.57D) broad, divided into 6 plumes, sometimes with narrow costal fold, hind wings with 6 or 7 plumes, wings rarely entire (South American species only); female with 2 frenular bristles; males sometimes with expandable pencil of long scales near base of anal plume of hind wing; T3–6 with narrow anterior band of spines. Eggs of flat type, cylindrical. Larva stout, ventral prolegs short with uniordinal crochets in complete circle; L1 and L2 approximate on abdominal segments 1–8, on separate oblique pinacula; tunnels in flowers, buds, fruits and shoots, sometimes producing galls. Pupa (Fig. 41.60I) with only segments 5 and 6 movable, tip with hooked setae, without cremaster; in cocoon on ground or in gall.

The adults of this small family with 6 named and several unnamed Australian species are easily recognised by their broad, many-plumed wings which are spread out flat when the adults rest. All Australian species are placed in

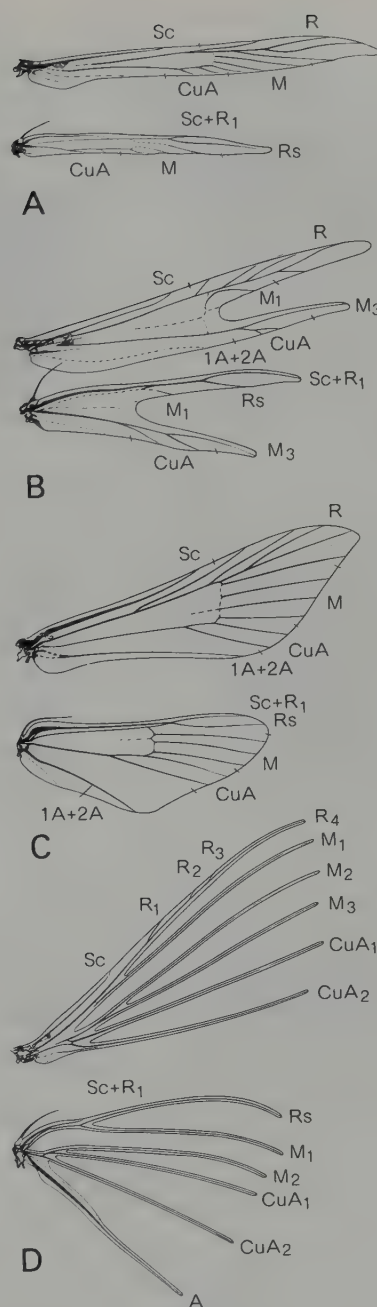


Fig. 41.57 Wing venation of Alucitoidea: A, *Oxychirota*, B, *Cenoloba*, C, *Tineodes*, Tineodidae; D, *Alucita*, Alucitidae. [J. Wedgbrow]

*Alucita*. *A. phricodes* (Fig. 41.56F) occurs in eastern Qld and N.S.W.; its larvae feed in flowers and flower buds of *Pandorea*. The larvae of *A. pygmaea* from Qld and the N.T. feed in the fruits of *Canthium oleifolium*. A large, unnamed species known from northern Qld., and north-western W.A. has larvae which form large, elliptical stem-galls in *Canthium* sp.

#### Superfamily PTEROPHOROIDEA

**57. Pterophoridae** (plume moths) (Fig. 41.58A). Small; head usually smooth scaled; ocelli and chaetosemata absent; antennae filiform; proboscis unscaled; max-

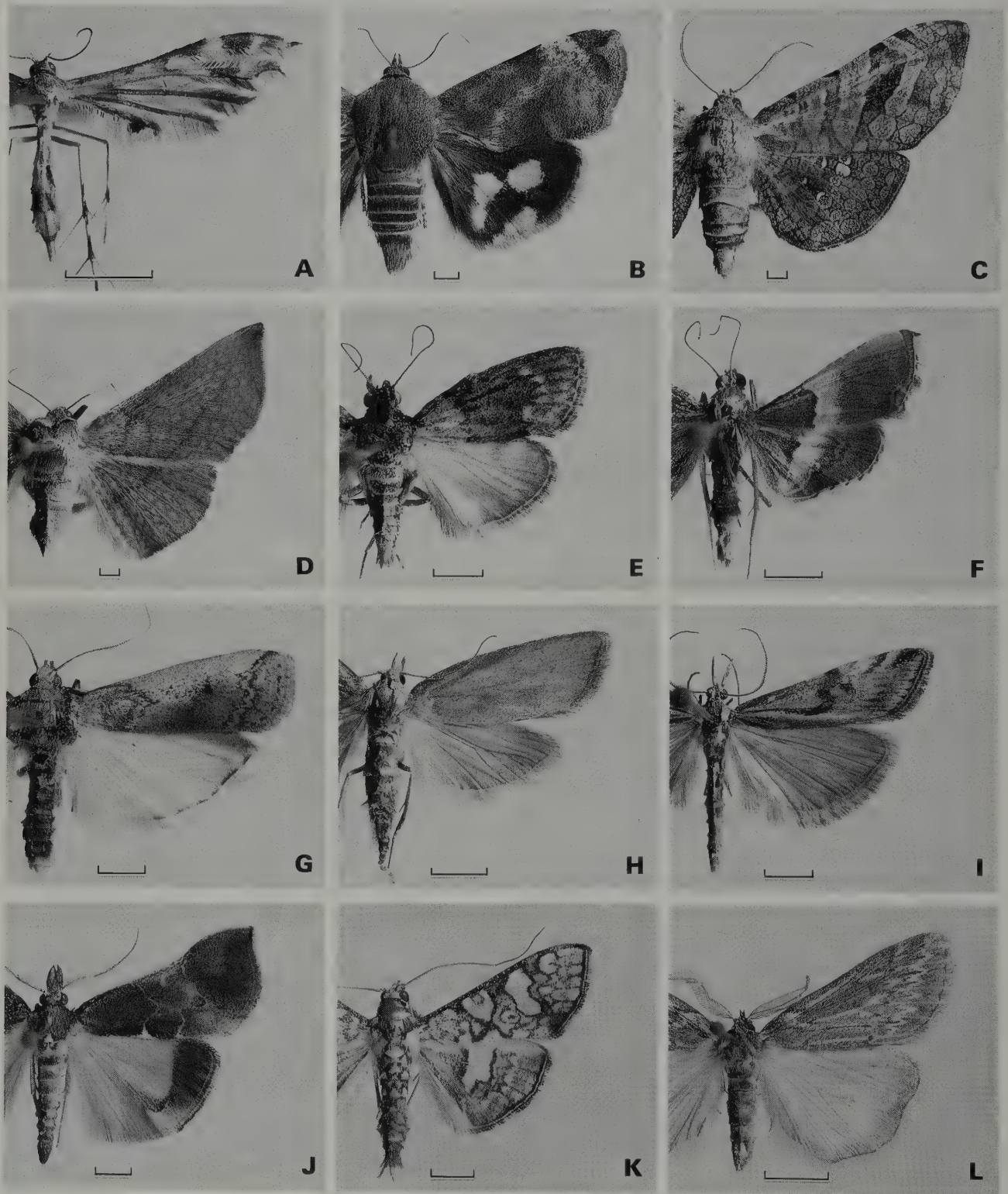


Fig. 41.58 A, *Sphenarches anisodactylus*, Pterophoridae; B, *Hyblaea puera*, Hyblaeidae; C, *Oxycophina theorina*, D, *Aglaopus pyrrhata*, Thyrididae; E, *Mimaglossa nauplialis*, F, *Endotricha mesenterialis*, G, *Cactoblastis cactorum*, H, *Callionyma sarcodes*, I, *Hednota pedionoma*, J, *Anemosa exanthes*, K, *Glyphodes canthusalis*, Pyralidae; L, *Ciampa arietaria*, Geometridae. Scales: A, E–K = 3 mm; B–D = 2 mm.

[C. Lourandos]



illary palps minute, 1-segmented; labial palps slender or stout, porrect or upturned; legs long, slender; epiphysis present; spurs 0-2-4, prominent; hind tibiae sometimes with specialised scaling; fore wing (Figs 41.59A, B) divided by terminal clefts into 2 or 3 plumes, rarely 4 plumes, or entire; with complex wing-folding mechanism (Wasserthal 1974), pterostigma sometimes present, wing-locking microtrichia absent, chorda and M absent in cell, one branch of R often absent,  $M_1$  and  $M_2$  weak or absent, CuP usually present, 1A+2A without fork; hind wing deeply cleft into 3 plumes, rarely entire, underside with double series of specialised scales along  $M_3$  and  $CuA_2$  or  $CuA_1$ , CuP absent, female frenulum of 1 or 2 bristles; abdomen long and slender, tympanal organs absent. Eggs of flat type, oval, smooth. Larva usually with numerous secondary, often modified setae, sometimes on verrucae, prothorax with 3 L setae, ventral prolegs long, crochets uniordinal in mesoseries or mesal penellipse; larvae usually leaf-mining at first, later exposed, eroding surface of leaves or burrowing in flower buds or in stems. Pupa (Fig. 41.60j) slender, smooth or spined, often with numerous setae on head, thorax and abdomen, pilifers present; fully exposed, attached by hooked setae on underside of abdominal segments 9 and 10.

Adult plume moths fly weakly and are usually found in the vicinity of their host plants; they come to light but can readily be disturbed during the day. They rest raised on the long fore and mid legs with the body horizontal and wings outspread.

The family is usually divided into three subfamilies all of which are represented in Australia. However, Wasserthal (1970) recognised 4 subfamilies.

AGDISTINAE have undivided fore and hind wings. *Ochyrotica kurandica* is known from northern Qld only. *Agdistopsis halieutica* occurs in the N.T. and Qld; larvae feed on fruit of *Secamone*.

PLATYPTILINAE have 3 veins in the second lobe of the hind wing and 1 vein in the third (Fig. 41.59A); the cilia are usually mixed with dark scales. Species of *Cosmoclostis* are particularly handsome, with silvery abdominal blotches and white and red-brown fore wings; 2 species occur in eastern Australia. *Stangeia xerodes*, which occurs widely in Australia, has larvae feeding on *Acacia* foliage. *Stenoptilia zophodactyla* occurs from Europe through Asia to Australia and New Zealand; its larvae feed on flowers of *Gentianella*. *Platyptilia omissalis* occurs widely in southern Australia and has larvae which first mine and later feed exposed on leaves of *Parahebe perfoliata*.

PTEROPHORINAE have 2 veins in both the second and third lobes of the hind wing (Fig. 41.59B), and the cilia are not mixed with scales. The pale larvae of the white *Pterophorus aptalis* feed on the underside of the leaves of *Astrotricha*.

### Superfamily HYBLAEIOIDEA

**58. Hyblaeidae** (Fig. 41.58B). Medium sized; head smooth scaled; ocelli present; chaetosemata absent; antennae filiform; proboscis strong, naked; maxillary palps short, 3- or 4-segmented, with long scales; labial

palps porrect, beak-like; epiphysis present; tibial spurs 0-2-0 in male, 0-2-4 in female, hind tibia in male with long projecting apical lobe and hair-pencil which folds into a specialised, bladder-like appendage from the hind coxa, tarsi strongly spined beneath; fore wing (Fig. 41.59C) with retinaculum in male a long slender hook on Sc, chorda and M stem absent from cell, all veins separate,  $M_2$  arising nearer to  $M_3$  than  $M_1$ , CuP absent, 1A and 2A not fused, 1A strong, 2A sinuous and not reaching margin; hind wing with 3 frenular bristles in female, Sc fused with Rs near base of cell, thence divergent,  $M_2$  arising nearer to  $M_3$  than to  $M_1$ , CuP a weak tubular vein near margin, 2 anal veins; tympanal organs absent; uncus simple or trifid. Eggs of flat type. Larva stout, without secondary setae, prothorax with 2 L setae, prolegs short, crochets bi- or triordinal in a circle; in shelter between joined leaves. Pupa (Fig. 41.60k) stout, with distinct maxillary palps, antennae short, epicranial suture distinct, without dorsal abdominal spines, cremaster present; in silken cocoon among foliage, fallen leaves, or in soil.

This small family, with only 2 genera in tropical America and Indo-Australia, has previously been variously associated with the Noctuoidea, Pyraloidea and even the Sesiioidea.

The absence of tympanal organs, and the structural characters of both larvae and pupae separate the Hyblaeidae from both Pyraloidea and Noctuoidea. The larvae of *Hyblaea puera* (Fig. 41.58B) feed on Verbenaceae, defoliating teak in Java and New Guinea, and in northern Australia are found on *Vitex trifolia*, living in shelters formed by folding the leaves. The uncus of the male is trifid, whereas in *H. ibidias* it is simple. The larvae of *H. ibidias*, with habits similar to those of *H. puera*, feed on *Pandorea jasminoides* in central and southern Qld.

### Superfamily THYRIDOIDEA

**59. Thyrididae** (Figs 41.58C, D). Small to large; head smooth scaled; ocelli usually and chaetosemata always absent; antennae simple, dentate, or pectinate; proboscis present, naked, or rarely absent; maxillary palps minute, 1- or 2-segmented; labial palps porrect or recurved, sometimes very short and only 2-segmented; epiphysis present; tibial spurs 0-2-2, 0-2-3 or 0-2-4; male hind tibiae sometimes with expandable hair-pencil; fore wing (Fig. 41.59D) with retinaculum in male a long slender hook on Sc, without wing-locking microtrichia; chorda and M stem absent from cell, all veins often separate, CuP absent, 1A+2A with basal fork or 2A vestigial; hind wing with 2 or 3 frenular bristles in female, all veins separate, Sc sometimes connected to Rs by  $R_1$  and approximated to, or fused with, Rs beyond cell,  $M_2$  arising nearer to  $M_3$  than to  $M_1$ , CuP vestigial, 2 anal veins; tympanal organs absent. Egg of upright type. Larva without secondary setae, prothorax with 2 L setae, prolegs short, crochets uni- or irregularly biordinal, in circle or ellipse; tunnelling in twigs and stems, sometimes producing swellings, or in shelter between green leaves. Pupa with maxillary palps and pilifers defined, without dorsal abdominal spines; in silk-lined cell.

The family is almost entirely tropical or subtropical.

Although variable in size, the adults usually have a characteristic, fine, reticulated wing pattern (Figs 41.58C, D) and distinctive resting posture, with the body raised at a steep angle and the wings expanded. They differ from pyralids by the unscaled proboscis and absence of abdominal tympanal organs. Several of the genera occurring in Australia have a wide distribution through Asia and some occur in Africa. *Aglaopus pyrrhata*, one of the stout-bodied STRIGLININAE, occurs as far south as Melbourne; its larvae feed on *Eucalyptus*, first in a cone-shaped shelter, later in a folded leaf shelter or between joined leaves. *Addaea* (6 spp.) belongs to the SICULODINAE, in which Sc is fused with Rs beyond the cell in the hind wing. *A. subtessellata* occurs in southern Qld and N.S.W.; the larvae feed gregariously between joined leaves of *Mallotus philippensis*. *A. polyphoralis* from the N.T. and Qld has larvae feeding, also gregariously, between joined leaves of *Diospyros ferrea*. [Whalley 1976]

### Superfamily PYRALOIDEA

**60. Pyralidae** (Plate 7, M; Figs 41.58E–K). Small to large; head smooth scaled, sometimes with anterior tuft; ocelli and chaetosemata present or absent; antennae filiform and ciliated, rarely uni- or bipectinate; proboscis densely scaled near base, sometimes reduced or vestigial; maxillary palps scaled, usually 4-segmented, sometimes 2- or 3-segmented, rarely vestigial; labial palps correct, beak-like, or ascending, especially in male, rarely

reduced; epiphysis present, spurs 0-2-4, rarely 0-2-2; fore wing (Figs 41.59E, F) without chorda and M stem in cell, with  $R_3$  and  $R_4$  stalked or coincident,  $M_2$  approximated to  $M_3$  at base, CuP rarely present,  $1A+2A$  usually with large fork; hind wing of female with 1-3 frenular bristles,  $Sc+R_1$  approximated to, or shortly fused with, Rs beyond discal cell,  $M_2$  approximated to  $M_3$  at base, CuA sometimes with basal pecten, CuP rarely absent, anal area large, with 2 anal veins; tympanal organs present at base of abdomen, coremata often present. Eggs of flat type, usually oval. Larva usually without secondary setae, prothorax with 2 L setae, crochets usually bi- or triordinal, in a circle or mesal penellipse, rarely uni- or biordinal in 2 transverse bands; in Nymphulinae larvae adapted for aquatic life, respiration by means of filamentous gills or plastron or cutaneously; in shelters of webbed leaves or shoots, or tunnels in shoots, stems, seed heads, fruits or galls, or in silken galleries among mosses, herbaceous plants, or fallen leaves, or in shelters or cases among aquatic plants in fresh water, or in stored products, or in nests of Hymenoptera, rarely predacious on coccoids (HEMI). Pupa (Fig. 41.60L) with pilifers defined, maxillary palps present (except Epipaschiinae), antennae long, abdomen without dorsal spines, cremaster present or absent; in Nymphulinae abdominal spiracles may be reduced in number; in silken cocoon or in larval shelter, not protruded at ecdysis.

This is a large and ubiquitous family, with species

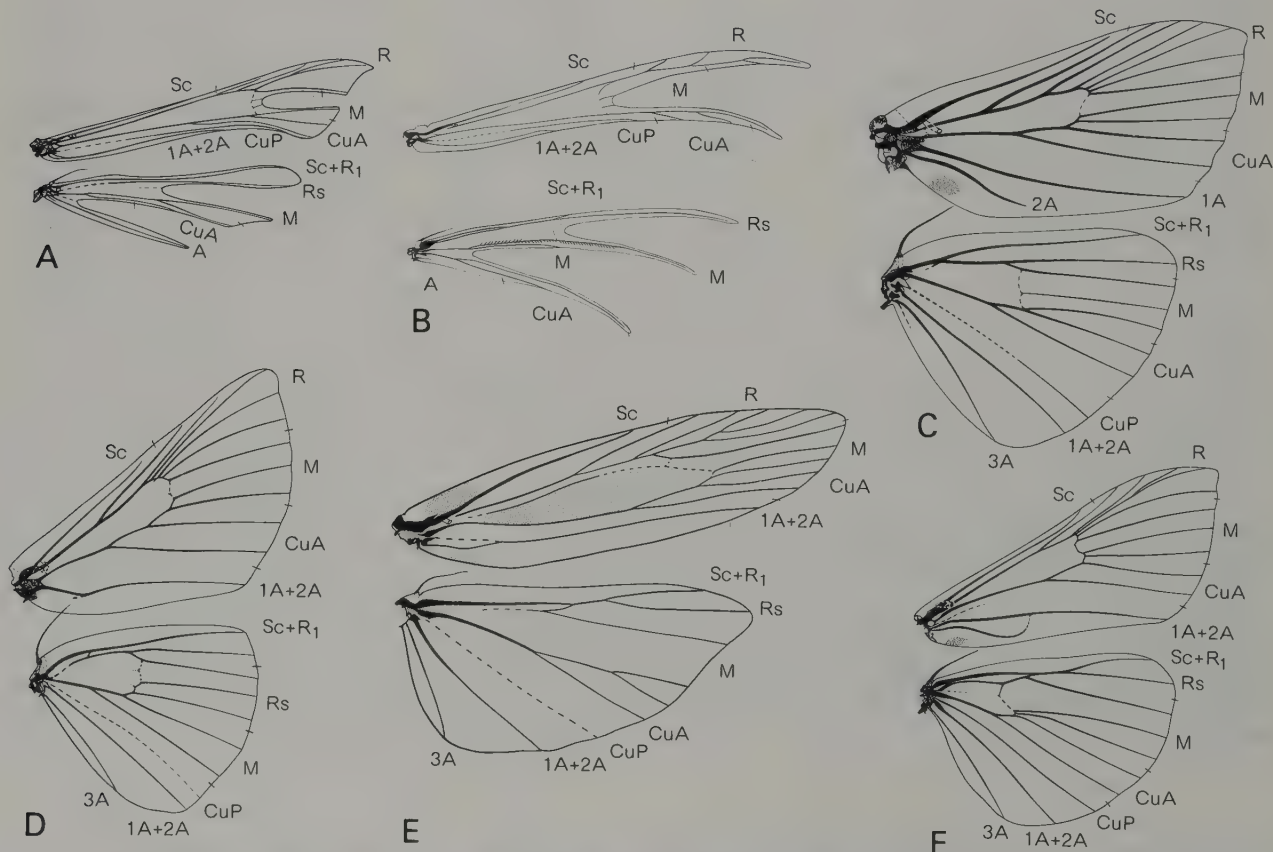


Fig. 41.59 Wing venation of Pterophoroidea, Hyblaeoidea, Thyridoidea and Pyraloidea: A, *Platyptilia*, B, *Pterophorus*, Pterophoridae; C, *Hyblaee*, Hyblaeidae; D, *Strigilina*, Thyrididae; E, *Meyriccia*, F, *Uresiphita*, Pyralidae. [A, C, D, F by J. Wedgbrow; B, E by I. F. B. Common]



adapted to diverse terrestrial and aquatic habitats. Many are pests of cultivated plants and stored products. Several subfamilies are recognised, and several authors place them in two main divisions, sometimes given family rank, depending on the presence or absence of a praecinctorium (a ventrally expanded, medial flap anterior to the tympanal organs) and whether the tympanal organs are medially approximated or well separated. Subfamily classification and keys to subfamilies are provided by Munroe (1972), Roesler (1973), Minet (1981, 1985) and Yoshiyasu (1985).

**GALLERIINAE.** Ocelli and chaetosemata absent, labial palps shorter in male than in female, male tegulae with usually finely corrugated sound-producing organs (tymbals) (Spangler 1988), fore wings usually distally rounded, males with gland at base of fore wing, hind wing with cubital pecten, male without gnathos. Australia has a relatively rich galleriine fauna. The wax moths *Galleria mellonella* and *Achroia grisella*, and the rice moth, *Corcyra cephalonica*, a stored-product pest, have been introduced to Australia. The larvae of the native *Meyriccia latro* tunnel gregariously in the flower spikes of grass trees (*Xanthorrhoea*), those of *Callionyma sarcodes* (Fig. 41.58H) are found under loose bark on *Eucalyptus* trunks, and those of some species of *Tirathaba* (7 spp.) and *Stenachroia* (1 sp.) in the tunnels of wood-boring lepidopterous larvae and ant nests respectively. [Whalley 1964]

**EPIASCHIINAE** (Fig. 41.58E). Ocelli and chaetosemata present; male antenna with scale-covered projection on scape, directed posteriorly; male labial palps long and curved backwards over head, fore wing with raised scale-tufts; frenulum simple in both sexes; pupae without maxillary palps. This subfamily is relatively well represented in Australia by more than 70 named species. The larvae of several species, including some in *Macalla* (22 spp.) and *Catamola thyrsalis*, live gregariously between webbed leaves of *Eucalyptus*, *Leptospermum* or *Melaleuca*. Those of the black *Stericta carbonalis* feed on dead *Eucalyptus* leaves. The larvae of *Titanoceros thermoptera* are predacious on egg masses of *Ochrogaster lunifer*.

**PYRALINAE** (Fig. 41.58F). Similar to Epipaschiinae, but the fore wing is without raised scale-tufts and the pupae have maxillary palps. This subfamily is also relatively well represented in Australia. The large agaristine-like *Vitessa* (3 spp.) occurs in Qld and the N.T. *Anemosa exanthes* was previously placed in the Chrysauginae but it has maxillary palps; the larvae feed on *Eucalyptus* leaves. Larvae of *Gauna aegusalis* burrow in galls on wattles (*Acacia* spp.). The meal moth *Pyralis farinalis* is an introduced pest of stored cereals.

**PHYCITINAE.** Fore wing with only 4 branches of R, proboscis present and hind wing with pecten at base of CuA, males with coremata. *Cactoblastis cactorum* (Fig. 41.58G) is undoubtedly the most famous phycitine; it was introduced to Australia from Argentina and successfully controlled the introduced prickly pear cactus, *Opuntia*; the larvae are bright orange-red with black transverse bars. Three Australian species of *Etiella* (7 spp.) (Whalley 1973) feed on the seeds of legumes; *E. behrii* is a pest of lucerne. Males of *Hypargyria metalliferella* have reflective, silvery scales on the underside of the wings;

the larvae live in a web on *Siphonodon australe*. Larvae of *Creobota coccophthora* feed on *Eriococcus* scale insects on *Eucalyptus*. Introduced pests of stored products include *Ephestia kuehniella*, *E. elutella*, *Cadra cautella*, *C. figulilella* and *Plodia interpunctella*.

**PEORIINAE.** Fore wing with 4 branches of R, as in Phycitinae, proboscis reduced or absent, male uncus spined and female ovipositor compressed. The Australian fauna consists of 17 named and many unnamed species. *Lioprosopa* (13 spp.) is probably the largest Australian genus.

**CRAMBINAE.** Maxillary palps prominent, dilated distally with scales, labial palps long and porrect, hind wing with pecten at base of CuA; larvae usually feed on grasses and other herbaceous monocotyledons, living in silk tubes in the crown of the tussock. *Hednota* (Fig. 41.58I) (60 spp.) is the largest Australian genus. Most species occur in southern mainland Australia and Tas.; some are plentiful locally and cause damage to grass pastures and cereal crops. Hosts include *Lomandra*, *Patersonia*, *Dasyopogon* and many grasses.

**NYMPHULINAE** (Acentropinae) have ocelli and chaetosemata, a long proboscis, usually pale wings with transverse patterns and silvery spots along the margin of the hind wing. The aquatic larvae are found in stagnant water and slowly or rapidly flowing streams. They may be case making, web spinning or free living, and feed on algae or aquatic plants. Many have filamentous gills and reduced spiracles. The pupae have protruding spiracles which are often restricted in number. The larvae of *Blechnoglossa nitens* and *Parapoynx tullialis* have filamentous gills and live in flat cases formed from pieces of the food plant.

**MUSOTIMINAE.** Very similar to the Nymphulinae, but fore and hind wings have an incision in the termen. The larvae are terrestrial and feed on ferns. Both larvae and pupae have the normal number of spiracles; the pupal spiracles are not protruding. *Musotima* contains about 10 species in Australia. The larvae of *M. nitidalis* sometimes defoliate maiden-hair ferns, *Adiantum aethiopicum*.

**SCOPARIINAE** bear some resemblance to Crambinae; in the fore wing  $R_2$  is well separated from  $R_{3+4}$  and CuP is absent; the females have supernumerary frenular bristles. Most species have triangular grey or mottled fore wings, and the larvae feed in a slight silk web on lichens and in mosses on rocks and tree trunks. *Scoparia* (59 spp.) is the largest Australian genus.

**SCHOENOBIIINAE** have a reduced proboscis, and CuP is present in the fore wing; the females, which are usually white, have a dense anal mass of deciduous hair-scales used to cover the egg masses. The larvae tunnel in grasses, sedges and rushes. The larvae of the northern Australian *Scirpophaga innotata* bore in cultivated and wild rice. *Tipanea patulella* is usually found among *Juncus*.

**WURTHIINAE** are small, broad-winged moths, without ocelli, chaetosemata or proboscis; antennae bipectinate in male, filiform in female, with dense pecten; spurs 0-2-2. The larvae of one species in Java make portable cases in green tree ant nests and feed on the ant larvae and

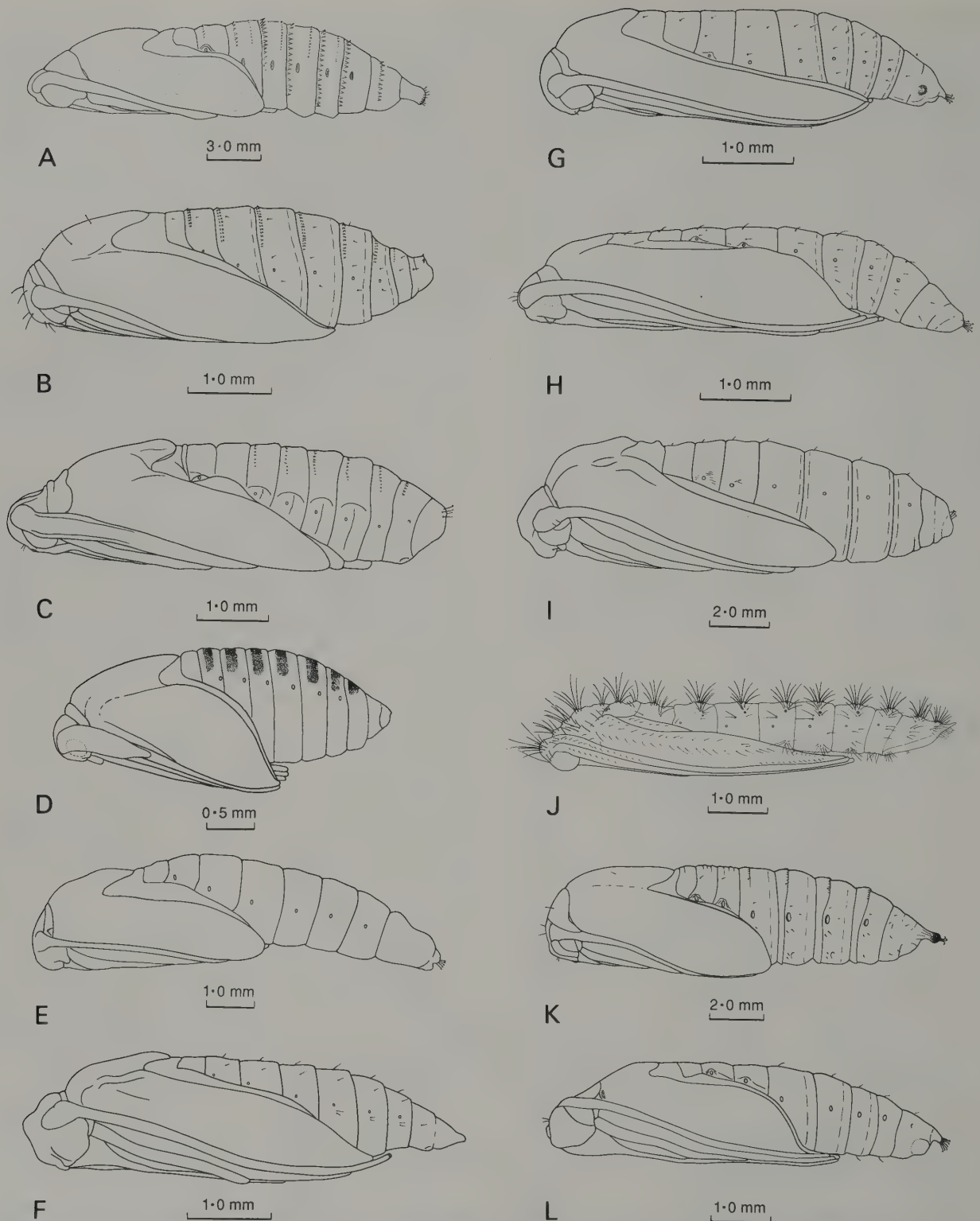


Fig. 41.60 Pupae of Castnioidea to Pyraloidea: A, *Synemon*, Castniidae; B, *Tebenna*, Choreutidae; C, *Onceropyga*, Zygaenidae; D, *Heteropsyche*, Epipyropidae; E, *Imma*, Immidae; F, *Bondia*, Carposinidae; G, *Gnathifera*, Epermeniidae; H, *Palaeodes*, Tineodidae; I, *Alucita*, Alucitidae; J, *Pterophorus*, Pterophoridae; K, *Hyblaea*, Hyblaeidae; L, *Glyphodes*, Pyralidae.

[I. F. B. Common]

pupae. Pupation occurs within the case in the ant nest. Several species occur in northern Australia; *Niphopyralis chionesis* is the only named Australian species. [Roepke 1916]

CYBALOMIINAE are without chaetosemata, ocelli and proboscis. The larvae of *Styphlolepis agenor*, one of the largest Australian pyralids, bore in the trunks of *Capparis mitchellii* in inland southern Qld and northern N.S.W.



EVERGESTINAE, with ocelli but without chaetosemata, are represented in Australia by *Crocidolomia* (3 spp.). The larva of *C. pavonana*, the cabbage cluster grub, feeds gregariously under a web on cabbages and other Brassicaceae in eastern Australia.

ODONTIINAE often have strongly modified male genitalia. Gwynne and Edwards (1986) demonstrated that *Syntonarcha iriastis* uses the modified genitalia for ultrasonic sound production.

GLAPHYRIINAE, with an unlobed praecinctorium, are a mainly New World subfamily represented in Australia by only 2 named species. Larvae of both *Hellula undalis* and *H. hydralis*, cabbage centre grubs, bore in the growing centre of cabbages and other Brassicaceae.

PYRAUSTINAE (Plate 7, M; Fig. 41.58K) are the largest Australian pyralid subfamily, containing many pest species. The adults have ocelli but lack chaetosemata, 1A+2A has a large fork, the praecinctorium is lobed and the moths often rest with the wings more or less expanded. The subfamily is most numerous in northern Australia; some species migrate long distances. The larvae usually live in webbed shelters among foliage. *Metallarcha* is endemic and occurs mainly in the dry inland. The larvae of the yellow peach moth, *Conogethes punctiferalis*, burrow in many different fruits; those of the cucumber moth, *Diaphania indica*, damage cucumbers and melons; *Herpetogramma licarsisalis* is a pest of pastures and lawn grasses. The larvae of *Ostrinia furnacalis* are a minor pest of rhubarb; and those of the widely distributed *Sceliodes cordalis* damage egg-fruit and the fruits of related plants. The larvae of *Uresiphita ornithopteralis* feed on the foliage of many legumes.

### Superfamily GEOMETROIDEA

**61. Geometridae** (Figs 41.58L, 61A–C). Small to large; head usually smooth scaled; ocelli usually absent; chaetosemata present; antennae simple or pectinate; proboscis present, unscaled; maxillary palps very small, 1- or rarely 2-segmented; labial palps usually small, upturned or correct; epiphysis present; spurs usually 0-2-4; male hind tibiae sometimes modified; wings broad, sometimes reduced in females, fore wing often triangular, discal cell rarely to beyond midlength, often with 1 or 2 areoles; fore wing (Figs 41.62A, B) with Sc close to or partly fused with  $R_1$ ,  $R_4$  and  $R_5$  always stalked,  $M_2$  not arising nearer to  $M_3$  than  $M_1$ , CuP absent, 1A+2A sometimes with small basal fork; hind wing with 2 or more frenular bristles in female, humeral angle usually expanded, humeral vein often present from angle of Sc, Sc approximated to, or fused with,  $R_s$  near base, or joined to  $R_s$  by  $R_1$ , and then divergent,  $M_2$  not arising nearer to  $M_3$  than  $M_1$  or absent, anal area narrow, 1 or 2 anal veins; abdomen often slender; paired tympanal organs present in invaginations of the anterior part of S2, inner side of each tympanal membrane with a thickened border and a sclerotised arm (ansa), with 4 acoustic sense cells. Larva (Figs 41.63A–C) usually long and slender, ventral prolegs sometimes present on segments 3–6, 4–6, 5 and 6 or, more usually, only 6, prolegs on 6 often posterior, anal prolegs massive; crochets biordinal in curved mesoseries, rarely uniordinal;

prothorax with 2, rarely 3, L setae; often twig- or leaf-like, rarely in loose shelter, usually feeding fully exposed. Pupa (Fig. 41.63D) with cremaster well developed, often with hooked setae; without dorsal spines; usually in flimsy cocoon in debris or in soil; not protruded at ecdysis. [McFarland 1988]

Most adult geometrids are nocturnal and rest during the day with their cryptic-coloured wings spread out and closely appressed to the surface. Larentiinae are often diurnal, particularly in subalpine areas. The reduced number of ventral prolegs results in the larvae progressing with a looping motion, hence the name loopers. McGuffin (1988) provides keys to subfamilies.

ARCHIEARINAE are day flying with brightly coloured hind wings and cryptic fore wings. The subfamily contains a few boreal Northern Hemisphere species, some southern Andean species and 4 species in Tas.: *Acalyphes philorites* and *Dirce* (3 spp.). In Tas. they are restricted to alpine and subalpine areas, where the adults fly in sunshine during spring and summer. The larvae of *Dirce* lack ventral prolegs on segments 3–5.

ENNOMINAE (Boarmiinae) are the largest geometrid subfamily in Australia.  $M_2$  is reduced or lost as a tubular vein in the hind wing, and males often have a fovea, a raised blister-like area of the wing-membrane, between CuA and 1A+2A at the base of the fore wing. In the larvae prolegs may be present on abdominal segments 3–6, or are absent on 3, 3 and 4 or 3, 4 and 5. In *Mnesampela* (7 spp.) (McQuillan 1985b), which lacks a fovea, the larvae have 4 pairs of prolegs (Fig. 41.63A) increasing in size from segment 3 to 6, all with uniordinal crochets in a circle. Larvae of *M. privata* feed on the juvenile foliage of *Eucalyptus* and can seriously defoliate young plants; the young larvae are gregarious but later larvae live usually 2 or 3 together, in loose shelters. The greyish, narrow-winged *Chlenias* (21 spp.) occur in south-eastern mainland Australia and Tas.; the larvae are polyphagous and some species attack the introduced *Pinus radiata*. *Ciampa arietaria* (Fig. 41.58L) is a minor pest of pastures, where the larvae usually feed on *Erodium* and other low plants. *Thalaina* (Fig. 41.61A; 10 spp.) includes striking, satin-white species with distinctive patterns (McQuillan 1981); the larvae have ventral prolegs on segments 4, 5 and 6 and feed on *Acacia*. The adults of many genera have cryptic wing patterns of wavy, transverse lines and often rest on bark during the day; the males often have bipectinate antennae and a fovea, and the ventral prolegs of the larvae are reduced to one pair on segment 6. *Pholodes sinistraria* has polyphagous larvae which feed on many cultivated plants.

OENOCROMINAE are best developed in Australia where there are about 250 named species. In this probably polyphyletic subfamily are placed a cohesive group of stout-bodied moths (*Oenochromiina s.str.*), such as *Oenochroma*, and a group of perhaps unrelated slender-bodied species, such as *Nearcha* (14 spp.) and *Taxeotis* (45 spp.) (Scoble and Edwards 1990). Like the Ennominae, they are best represented in southern Australia. The larvae never have more than 2 pairs of ventral prolegs. The larvae of most species of *Oenochroma* (19 spp.), with 2



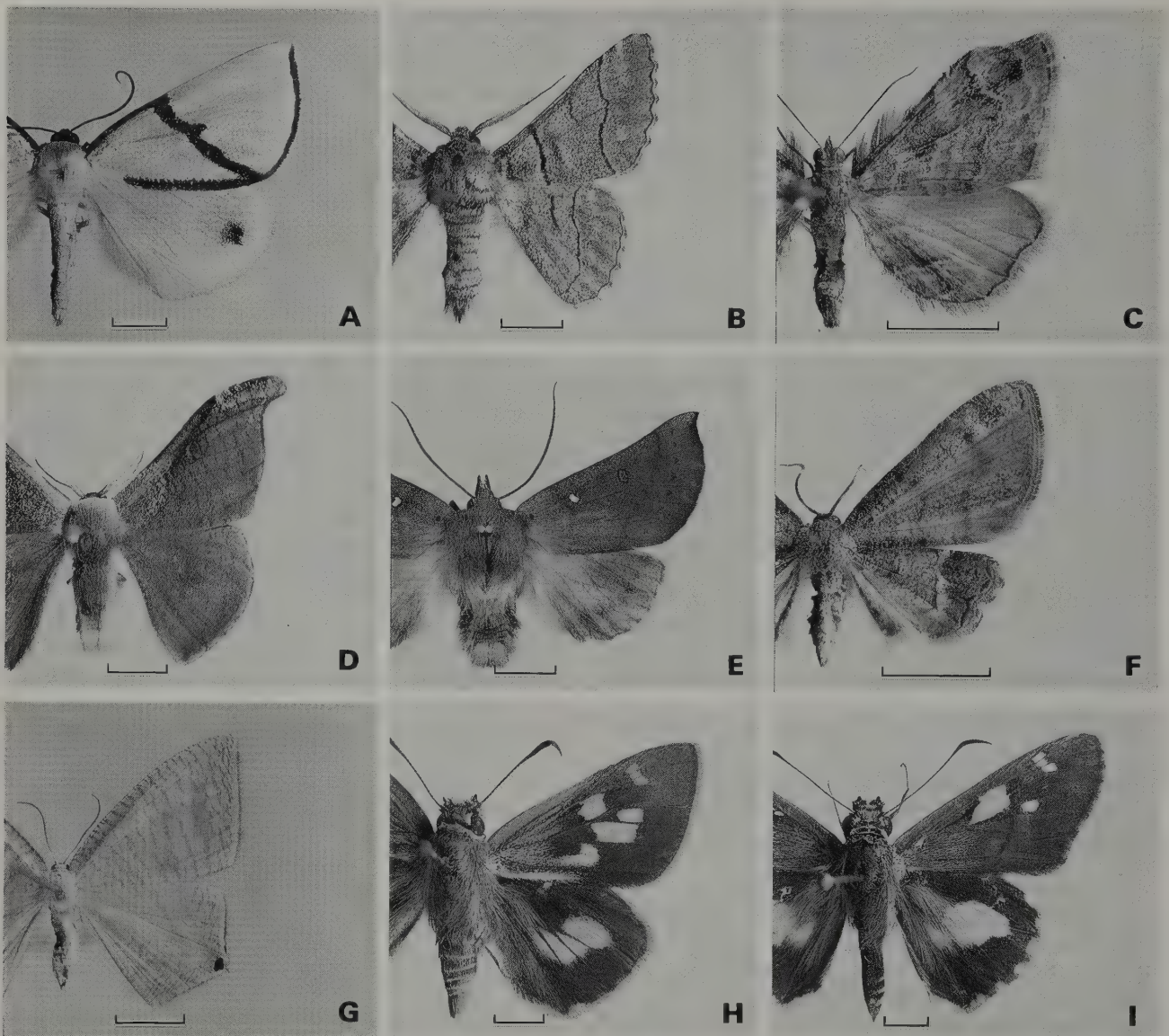


Fig. 41.61 A, *Thalaina selenaea*, B, *Hypobapta eugramma*, C, *Chloroclystis approximata*, Geometridae; D, *Oreta jaspidea*, E, *Hypsidia niphosema*, Drepanidae; F, *Lobogethes interrupta*, G, *Acropteris nanula*, Uraniidae; H, *Trapezites eliena*, I, *Hesperilla mastersi*, Hesperidae. Scales: A–G = 5 mm; H, I = 3 mm. [J. Green, C. Lourandos]

pairs of ventral prolegs (Fig. 41.63B), feed on Proteaceae, those of *O. vinaria* mainly on *Grevillea* and *Hakea*. Larvae of the striking, large *Gastrophora henricaria*, known from southern Qld to S.A., feed on *Eucalyptus* and *Leptospermum*. *Hypographa* (4 spp.) is also stout-bodied and has the termen of the wings deeply dentate. *Dichromodes* (65 spp.) is the largest of the slender-bodied genera; the larvae of some feed on shrubby Myrtaceae but not *Eucalyptus*. *Epidesmia* (10 spp.), with long and porrect labial palps, rests on the ground; the larvae of the common *E. chilonaria* probably feed on the foliage of woody Myrtaceae. *Taxeotis* adults also rest on the ground among leaf litter.

GEOMETRINAE (emeralds) include both stout- and slender-bodied genera; in the fore wing  $R_1$  is usually separate from  $R_2$  but fuses for a distance with Sc and in the

hind wing  $M_2$  arises closer to  $M_1$  than to  $M_3$ ; S3 often has patches of deciduous setae; the mature larvae have only one pair of ventral prolegs (Fig. 41.63C).

Most robust species, such as *Hypobapta eugramma* (Fig. 41.61B), have a cryptic grey pattern; its larvae have a conical head and are blue-green in colour matching the *Eucalyptus* leaves on which they feed. Species of *Aeolochroma* (14 spp.) have a strongly cryptic, moss-like pattern; the larvae of *A. metarhodata* feed on *Leptospermum flavescens*. The Oriental genus *Pingasa* reaches eastern Australia with 8 named species; the larvae of *P. chlora* feed on *Flindersia schottiana*. Many slender-bodied species have green wings. *Anisozyga pieroides*, (Plate 8, L) from the N.T., Qld and northern N.S.W., has well-camouflaged, polyphagous larvae with dorsolateral flanges. At least two handsome, named species of



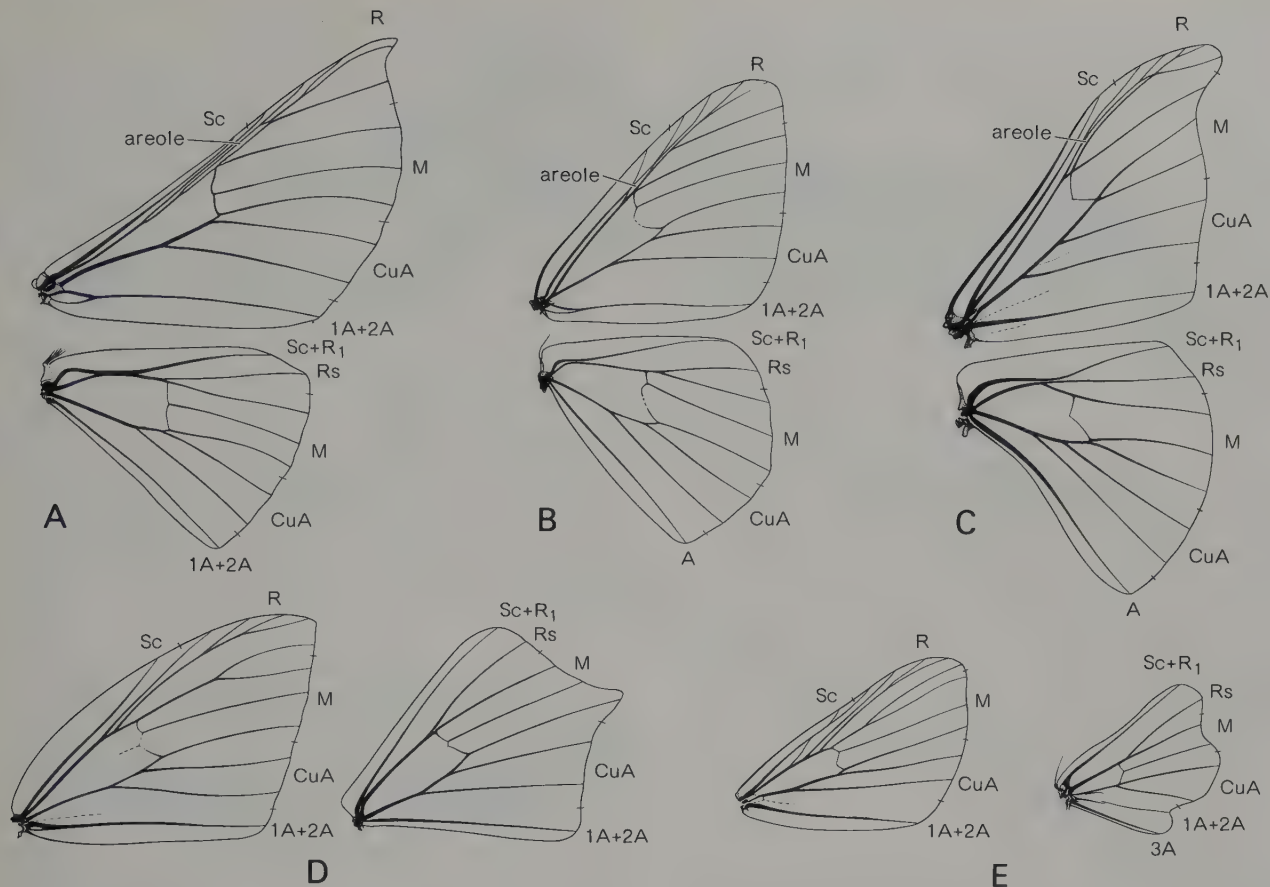


Fig. 41.62 Wing venation of Geometroidea, Drepanoidea and Urnioidea: A, *Oenochroma*, B, *Chlorocoma*, Geometridae; C, *Oreta*, Drepanidae; D, *Aploschema*, E, *Lobogethes*, Urniidae. [A by I. F. B. Common; B-E by J. Wedgwood]

*Agathia* occur in northern Australia. *Euloxia* (10 spp.) lacks a frenulum in both sexes and occurs mainly in south-eastern Australia including Tas.; the larvae feed on several plants, including *Nothofagus*.

STERRHINAE include mainly small, delicate, often pink or yellowish species with multifasciate fore wings. In the fore wing Sc is separate from the branches of R and 1 or 2 areoles are nearly always present. In the hind wing Sc fuses with Rs for a short distance towards the base before diverging sharply. *Anisodes* (25 spp.) is widely distributed in the Oriental and Australian regions; the green larvae of *A. turneri* feed on *Glochidion lobocarpum* and the pupa is attached beneath a leaf of the food plant by the cremaster and a silk girdle around the abdomen. The widely distributed genus *Scopula* (28 spp.) contains many very similar species with fine transverse lines.

LARENTIINAE have strongly marked fore wings with wavy, transverse lines and fasciae that tend to meet the dorsum at right angles in the fore wings. In the fore wing Sc is separate from the branches of R and 1 or 2 areoles are present. In the hind wing the base of the costa is strongly expanded and Sc is sharply bent at the base and then usually fuses with Rs to well beyond half of the cell before diverging; the hind wings are sometimes modified or reduced. Many species are day-flying especially in subalpine localities. *Xanthorhoe* (20 spp.) and *Euphyia*

(63 spp.) are found in Tas. and the highlands of Vic. and N.S.W. Males of *Microdes* usually have a patch of specialised scales on the hind wing and the larvae feed on *Acacia* species. In *Sauris* (Dugdale 1980) the hind wings are distorted in males and the hind tibiae lack spurs. Species of *Chloroclystis* (Fig. 41.61C; 30 spp.) and *Gymnoscelis* (17 spp.) are small with larvae feeding on flowers.

### Superfamily DREPANOIDEA

**62. Drepanidae** (Figs 41.61D, E). Small to medium sized; head usually smooth scaled; ocelli present or absent; chaetosemata absent; antennae filiform, lamellate or bipectinate; proboscis present and unscaled, or absent; maxillary palps minute, 1-segmented or absent; labial palps short to long, porrect or upcurved; epiphysis present or absent; spurs 0-2-4, 0-2-2, 0-0-4 or 0-0-0; tarsal claws usually toothed, hind tibiae often with long scales; fore wing (Fig. 41.62C) usually broadly triangular, apex often falcate, with or without wing-locking microtrichia, often with one narrow areole, CuP absent, 1A+2A sometimes with short fork; frenulum often clubbed or absent; Sc+R<sub>1</sub> separated from Rs at base, approximated to, or shortly fused with, Rs before or beyond end of cell, CuP absent, 1 or 2 anal veins; abdomen with paired, 2-chambered tympanal organs in segment 2 with tympanum situated

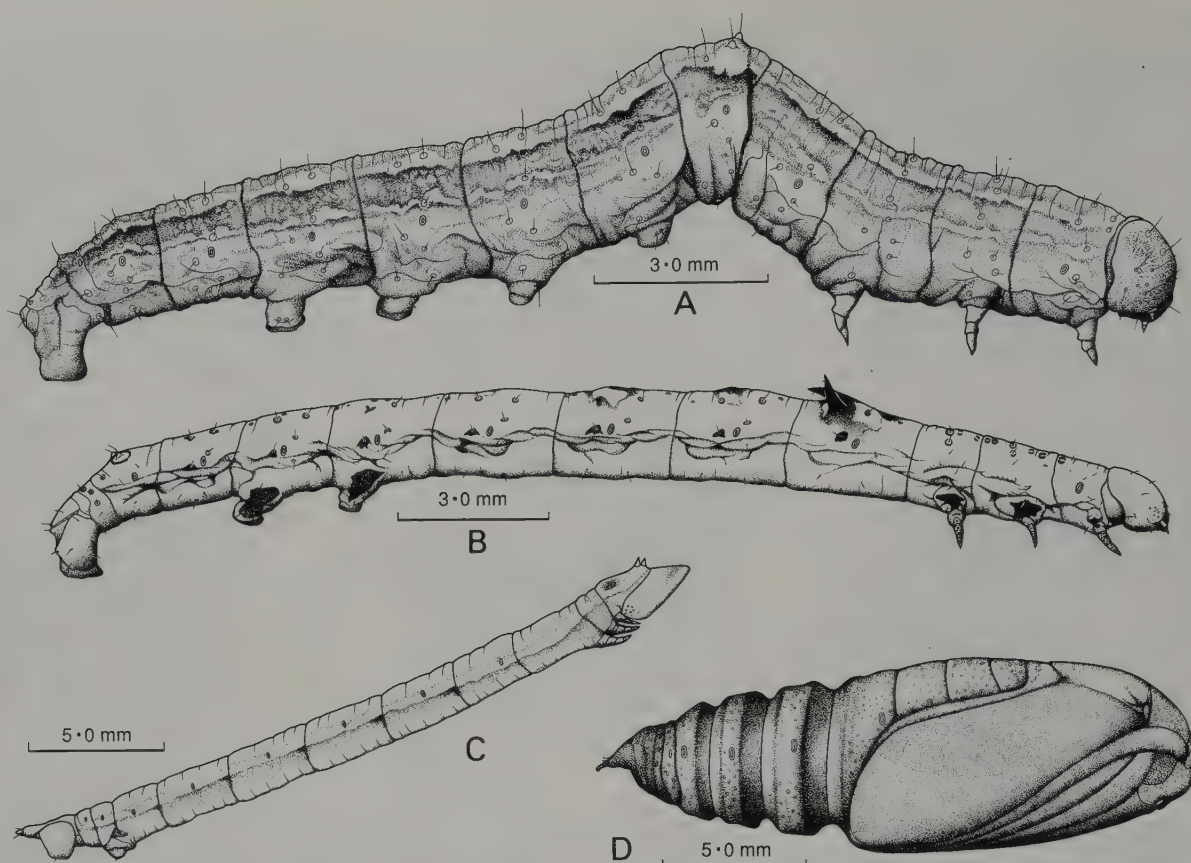


Fig. 41.63 Larvae and pupae of Geometridae: A, larva of *Mnesampela*; B, larva of *Oenochroma*; C, larva of *Chlorocoma*; D, pupa of *Melanodes*.

[J. Wedgbrow]

within a sternal component between chambers. Eggs of flat type. Larvae with ventral prolegs on segments 3 to 6 with bi- or, rarely, uniordinal crochets in a mesoseries and, usually, a small uniordinal lateroseries; anal prolegs reduced or absent, secondary setae present or absent; exposed or in rolled leaf, with end of abdomen sometimes produced and raised when resting. Pupa without dorsal spines, cremaster rudimentary, in cocoon among fallen leaves; not protruded at ecdysis.

The family contains the DREPANINAE, THYATIRINAE and CYCLIDIINAE; the Cyclidiinae are absent from Australia and adults of the two other subfamilies are difficult or impossible to classify (Scoble and Edwards 1988). The Australian fauna is small with 4 named species in 4 genera of typical hook-tip moths, Drepaninae, and 6 species in *Hypsidia*. The brown *Oreta jaspidea* (Fig. 41.61D), the largest Australian species, occurs in north-eastern Qld, while the yellow *Astatochroa fuscimargo*, the smallest species, is found in east Qld. *Hypsidia* includes 2 rainforest species in north-eastern Qld and 4 species in south-western W.A. (Fig. 41.61E); the immature stages of *Hypsidia* are unknown.

#### Superfamily URANIOIDEA

**63. Uraniidae** (Plate 8, I; Figs 41.61F, G). Small to large; head smooth scaled; ocelli absent; chaetosemata present, large; antennae thickened, dentate or pectinate in

male, filiform in female; proboscis present, unscaled; maxillary palps minute, 1-segmented; labial palps small, slender, upturned; epiphysis present; spurs 0-2-3 or 0-2-4; fore wing (Figs 41.62D, E) without wing-locking microtrichia,  $R_5$  well separated from other branches of R and usually stalked with  $M_1$ , CuP absent,  $1A+2A$  sometimes with minute fork; hind wing with or without frenulum, and with or without tails,  $M_2$  widely separate from  $M_3$ , CuP absent, 1 or 2 A veins; abdomen with dimorphic paired tympanal organs situated laterally between  $S_2$  and  $S_3$  in male and at base of  $S_2$  in female (Minet 1983). Eggs of upright type. Larva with prolegs on segments 3-6 and 10, secondary setae few or absent, prothorax with 2 L setae, setae on raised pinacula, spiracles on prothorax and abdominal segment 8 much the largest; external feeder. Pupa with dense cover of fine punctures on abdomen, segments 5 and 6 movable, without dorsal spines, with pointed cremaster and divergent anal spines; in cocoon; not protruded at ecdysis.

The rather dissimilar subfamilies Uraniinae, Microniinae and Epipleminae are firmly united by their unique dimorphic tympanal organs.

URANIINAE have no frenulum, but have a weak humeral vein and one anal vein in the hind wing; the female tympanal organs are protected by covers formed from the metathorax. Some species are large, diurnal and butterfly-like with prominent tails. The adults of *Alcides zodiaca*



(Plate 8, I), from rainforest in northern Qld, feed at flowers and rest with wings outspread; sometimes, towards evening, they fly high above the forest and migratory flights have been reported. The larvae have black and white bands and feed on the leaves of the vines *Omphalea* and *Endospermum*. The Oriental and Papuan *Lyssa patroclus* with long tails is nocturnal; it occurs in northern Qld rainforest and has larvae feeding on *Endospermum medullosum*. [Monteith and Wood 1987]

MICRONIINAE usually lack a frenulum, have a weak humeral vein in the hind wing and one anal vein, and the female tympanal organs are protected by projecting coxal scales. The adults of the 6 Australian species are delicate, mainly white, rainforest insects, with fine, pencilled markings and with a dark spot on a tail or angle at the end of  $M_3$  on the hind wing. They are nocturnal, have a slow flight and rest with wings outspread. They occur in the N.T., Qld and northern N.S.W. *Micronia* (2 spp.) differs from the remaining genera by having  $R_5$  and  $M_1$  separate in the fore wing. *Aploschema discata* and *Acropteris nanula* (Fig. 41.61G) are found from south-eastern Qld to central N.S.W.

EPIPLEMINAE have Sc sometimes partly fused with  $R_1$  in the fore wing, hind wing frenulum present, humeral vein absent,  $Sc+R_1$  diverges from  $R_5$  at the base, there are 2 A veins, and the margin is irregular or short-tailed. The shape of the hind wing is sometimes sexually dimorphic. There are 26 named species in Australia. The hind wing usually has a fascia from the middle of the costa, running obliquely towards the end of  $M_3$ , then angling sharply back towards the tornus. At rest the hind wings are usually folded along the abdomen, whereas the fore wing is either rolled, curled or extended flat. Adults of *Balantiucha decorata* rest with the fore wings extended and rolled and the hind wings appressed along the abdomen, while those of *Lobogethes interrupta* (Fig. 41.61F) rest with both fore and hind wings extended and rolled; the larvae erode the underside of the leaves of *Canthium coprosmoides* and *C. oleifolium* respectively. The subfamily is mainly tropical in distribution but is known as far south as the A.C.T.

### Superfamily HESPERIOIDEA

**64. HesperIIDae** (skippers) (Plate 8, N; Figs 41.61H, I). Small to medium sized; head broad, with short slender scales; compound eye surrounded by row of small ommatidia; ocelli absent; chaetosemata present; antennae widely separated at base, scape with scale-tuft, flagellum gradually dilated apically to form club, usually with hooked tip; proboscis naked; maxillary palps absent; labial palps ascending; epiphysis present, spurs 0-0-4, 0-2-4, 0-2-2 or 0-0-2; fore wing (Figs 41.65A, B) without retinaculum (except male *Euschemon*), veins arising separately from cell, CuP absent,  $1A+2A$  simple or forming basal fork; hind wing with frenulum absent (except male *Euschemon*), humeral vein usually present, Sc connected to  $R_s$  near base by  $R_1$ , veins arising separately from cell, CuP absent, 2 anal veins. Egg of upright type, smooth or with vertical ribs. Larva (Fig. 41.66A) with primary setae obscured by abundant, fine, short, secondary setae; con-

stricted behind large head; crochets bi- or triordinal in a circle; in silk-lined shelter between joined leaves or in longitudinally rolled leaf. Pupa (Fig. 41.66B) in larval shelter, attached by cremaster and usually by a central silken girdle.

This homogeneous family is defined by the absence of stalked veins and the subapically thickened antennae (Kristensen 1976). Most species are diurnal, but a few are crepuscular. Their flight is rapid and rather jerky, and in repose the wings are held back to back, sometimes with the hind wings depressed, or are extended flat. The larvae of some species feed on dicotyledons, whereas most feed on monocotyledons. Six subfamilies are recognised (Ackery 1984) of which Pyrrhopyginae and Megathyminae do not occur in Australia. [Common and Waterhouse 1981]

COELIADINAE are fairly large with short antennae, apical segment of labial palps long and slender and directed forwards, hind wing distinctly lobed, tornus sometimes produced,  $M_2$  tubular and arising nearer  $M_1$  than  $M_3$ ; males sometimes with sex-brand on fore wing. The larvae are brightly coloured and feed on dicotyledons. The 7 Australian species in 3 genera all occur in eastern and northern Australia. *Allora* (2 spp.) has brilliant metallic blue-green at the base of the wings; in Australia it occurs only in north-eastern Qld where it is rarely collected. The larvae of *Hasora* (4 spp.) are known to feed on several species of Fabaceae.

PYRGINAE are large and robust, and have the wings expanded flat when at rest, apical segment of labial palps short and porrect,  $M_2$  in hind wing sometimes absent and mid tibiae sometimes without spurs. The larvae are brightly coloured and feed on dicotyledons. *Euschemon rafflesia* (Plate 8, N) is remarkable because of the presence of a frenulum and retinaculum in the male; the larva feeds and pupates between joined leaves of *Wilkiea macrophylla* and *W. huegeliana* in rainforest. The adults of *Chaetocneme* (4 spp.) are crepuscular, and often have bright red eyes. *Netrocoryne repanda* occurs from northern Qld to eastern Vic. and the larvae feed on plants belonging to several families.

TRAPEZITINAE are recognised by the M fork in the hind wing cell where the lower branch terminates at  $M_3$  rather than near  $M_2$ . The group is mainly Australian, and is most numerous in the south. The larvae feed on sedges, grasses and other monocotyledons, usually sheltering between two or three leaves joined with silk. In *Trapezites* (13 spp.) the larvae feed at night on *Lomandra*, hiding during the day at the base of the plant. *T. eliena* (Fig. 41.61H), with a large, white spot on the underside of the hind wing, occurs in coastal, eastern Australia. *Toxidia* (8 spp.) includes dull brown species, which also occur in the tropics. The larvae of *T. doubledayi* and other species feed on grasses. Swordgrass (*Gahnia*) is the food plant of *Hesperilla* (13 spp.), the finest of which is *H. mastersi* (Fig. 41.61I), which occurs mainly in coastal N.S.W. [Atkins 1984; Edwards 1987]

HESPERIINAE have  $M_2$  arising nearer  $M_3$  than  $M_1$  in the fore wing and the males lack hair-pencils on the metatibiae and a costal fold on the fore wing. The adults rest with



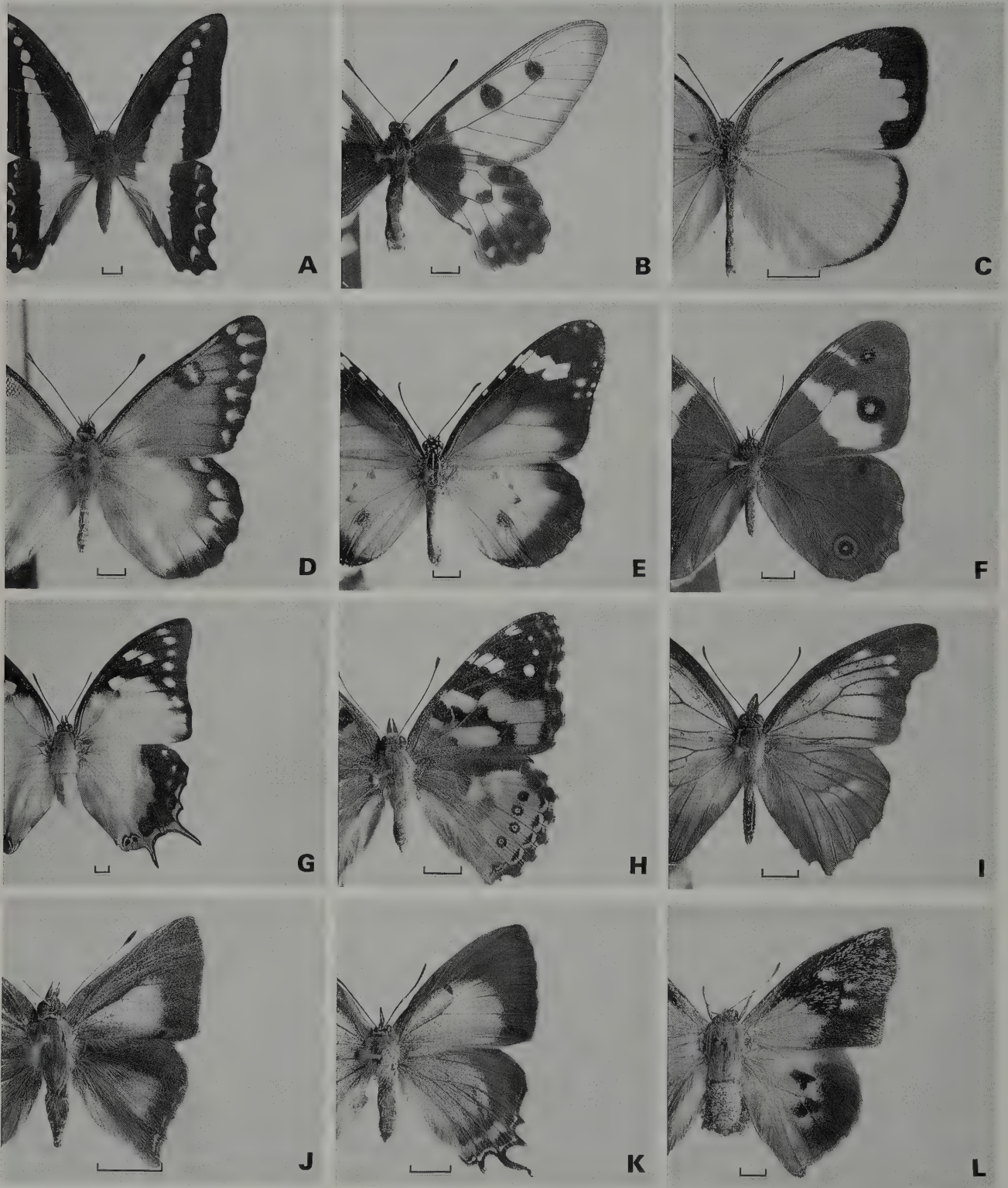


Fig. 41.64 A, *Graphium sarpedon*, B, *Cressida cressida*, Papilionidae; C, *Eurema hecabe*, D, *Delias aganippe*, Pieridae; E, *Danaus chrysippus*, F, *Tisiphone abeona*, G, *Polyura sempronius*, H, *Vanessa kershawi*, I, *Libythea geoffroy*, Nymphalidae; J, *Paralucia aurifera*, K, *Jalmenus evagoras*, L, *Liphyra brassolis*, Lycaenidae. Scales = 5 mm.

[C. Lourandos]



wings held erect. The subfamily is mostly tropical, with larvae feeding on coarse grasses and palms. *Taractrocera* (5 spp.) and *Ocybadistes* (4 spp.) contain small orange and black species frequenting long grass; the antennal club of the former is spoon-shaped. *Telicota* (8 spp.) has similar but larger species. *Pelopidas lyelli* is one of several rather similar, greenish grey-brown species from northern Australia.

### Superfamily PAPILIONOIDEA

Ocelli absent; chaetosemata prominent; antennae clubbed distally, without apical hook; proboscis naked; maxillary palps minute, 1-segmented, or absent; CuP usually absent from both wings, frenulum absent; tympanal organs absent. Egg of upright type. Larva with crochets in a circle in 1st instar, usually in a mesoseries in later instars. Pupa usually exposed and attached at posterior end to a pad of silk, and often with central silken girdle.

This superfamily, together with the Hesperioidea, constitutes the butterflies, or Rhopalocera, the monophyly of which is supported by several synapomorphies (Kristensen 1976). The geometrid-like Central and South American Hedyliidae were argued by Scoble (1986) to be the closest relatives of the Papilionoidea. Some authors regard the Papilionoidea as the most advanced Lepi-

doptera, and without doubt they are highly specialised. Nevertheless, such plesiomorphic characters as the presence of a short basal section of CuP and a separate 2A are retained in the fore wing of the Papilionidae and the 1st instar larvae have crochets in a complete circle, whereas in later instars they are progressively modified to a mesoseries; in the Bombycoidea, Sphingoidea and Noctuoidea, on the other hand, the crochets of all instars are arranged in a mesoseries. The butterflies are among the most popular groups of insects and the vast knowledge of their biology was recently summarised by Vane-Wright and Ackery (1984).

All papilionoid families are represented in Australia, especially in the tropics. New Guinea and Oriental genera predominate, but endemic genera occur in the Satyrinae and Lycaenidae. The most recent detailed account of the Australian fauna is that of Common and Waterhouse (1981).

Four families are usually recognised (Kristensen 1976) but studies of butterfly fore legs provide support for the view that Riodinidae (here in the Lycaenidae) and Libytheidae (here in the Nymphalidae) are monophyletic with and have the same rank as the Nymphalidae in an unresolved trichotomy and indicate that the Lycaenidae are diphyletic (Robbins 1988).

### Key to the Families of Papilionoidea

1. Fore tibia with epiphysis; fore wing vein 2A ends on dorsum ..... **Papilionidae** (p. 895)
- Fore tibia without epiphysis; vein 2A, when present, merges with 1A ..... 2
- 2(1). Tarsal claws bifid; ♂ fore leg with pretarsus and all 5 tarsomeres functional; abdomen without sclerotised, prespiracular bar in basal segment ..... **Pieridae** (p. 896)
- Tarsal claws rarely bifid, if bifid asymmetric; ♂ fore leg without pretarsus and usually with fewer than 5 tarsomeres; abdomen with a sclerotised, prespiracular bar in basal segment ..... 3
- 3(2). Chaetosemata elongate, parallel to margin of eye; antenna with 3 carinae (raised longitudinal ridges) ..... **Nymphalidae** (p. 897)
- Chaetosemata otherwise; antenna with a single, longitudinal groove or not grooved ..... **Lycaenidae** (p. 898)

**65. Papilionidae** (Figs 41.64A, B). Large; antennae short; maxillary palps reduced to tiny projection; labial palps appressed to frons; epiphysis present, fore leg fully developed but pulvilli and arolium reduced, spurs 0-2-2 or 0-0-2, tarsal claws usually simple; fore wing (Fig. 41.65C) with  $R_4$  and  $R_5$  usually stalked, CuP usually present near base (often said to be a cross-vein between CuA and 1A), 2 anal veins, 2A stalked with 1A, terminating on dorsum; hind wing with humeral vein present, Sc connected to Rs near base by  $R_1$ , 1 anal vein. Egg nearly spherical, smooth or with raised protuberances, usually laid singly. Larva (Fig. 41.66C) stout, often with paired fleshy dorsal processes, thorax sometimes humped; a forked, eversible osmeterium, which emits a pungent odour, can be extruded from dorsum of prothorax; crochets triordinal. Pupa (Fig. 41.66D) exposed, attached by cremaster to a silken pad and by a central girdle of silk, head sometimes bifid, or thorax with a median horn.

Three subfamilies Baroniinae, Parnassiinae and Papilioninae are recognised (Hancock 1983; J. S. Miller 1987). The Australian species all belong to the tribes Leptocircini, Papilionini and Troidini of the PAPILIONINAE,

and are chiefly tropical and subtropical. The Leptocircini, in which the mature larvae are usually smooth and green, sometimes with pairs of conical projections on one or more thoracic segments and on the terminal abdominal segment, include *Protographium* (1 sp.) and *Graphium* (6 spp.). *P. leosthenes* has long, straight tails to the hind wings; its pupa lacks the prominent, median thoracic horn found in *Graphium*. The pale blue and black *G. sarpedon* (Fig. 41.64A) is one of several tail-less species. The larva feeds mainly on Lauraceae and Monimiaceae, including camphor laurel (*Cinnamomum camphora*), *Cryptocarya*, *Litsea* and *Doryphora*. The cryptic green larva, with a slender yellow lateral stripe, may be detected, like other papilionid larvae, by the pungent odour emitted by the osmeterium. The green and black *G. macleayanum*, with clubbed tails, occurs along the eastern tablelands, and is the only species found in Tas.

The Papilionini have larvae with a series of paired, dorsal, fleshy spines, especially while young. They feed mainly on Rutaceae. *Papilio* (7 spp.), sometimes with a tail to the hind wing, is the only Australian genus. The large, sexually dimorphic *P. aegaeus* and the smaller *P.*

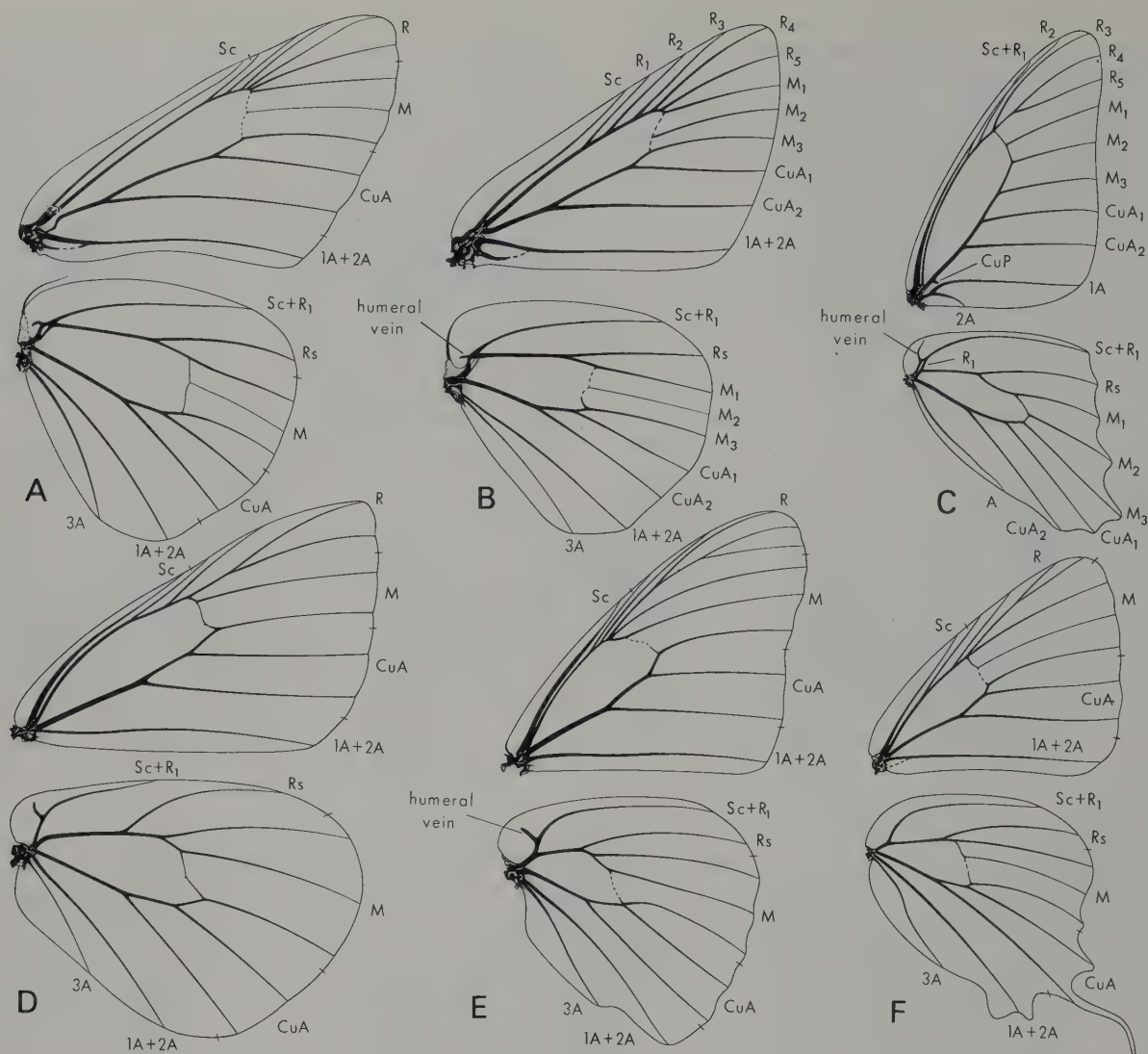


Fig. 41.65 Wing venation of Hesperioidea and Papilionoidea: A, *Euschemon*, ♂, Hesperidae; B, *Trapezites*, Hesperidae; C, *Graphium*, Papilionidae; D, *Pieris*, Pieridae; E, *Vanessa*, Nymphalidae; F, *Jalmenus*, Lycaenidae. [J. Wedgbrow]

*anactus* attack native Rutaceae and cultivated *Citrus*. The brilliant blue and black *P. ulysses* (Plate 8, K) occurs in New Guinea and northern Qld. The larvae are green with white markings, and feed on *Euodia*. The widely distributed Old World species, *P. demoleus*, is abundant in inland Australia. The larva is exceptional in feeding mainly on *Psoralea* (Fabaceae) although it also attacks *Citrus*.

The larvae of the Troidini, which feed on *Aristolochia*, have a series of soft, dorsal, often red protuberances. In *Cressida cressida* (Fig. 41.64B) the fore wing is largely hyaline, especially in the female, and the flight is slow. The predominantly Oriental troidine genus *Pachliopta* is represented in Australia by a single Papuan species *P. polydorus* which ranges south to tropical Qld. The largest and finest species is the sexually dimorphic Cape York birdwing, *Troides* (= *Ornithoptera*) *priamus* (see J. S. Miller 1987), with green, black and gold male and much larger, black, white and yellow female. There are 4

Australian subspecies. The smaller and duller *T. richmondia* occurs in southern Qld and northern N.S.W.

**66. Pieridae** (Figs 41.64C, D). Medium sized; maxillary palps absent; labial palps ascending, appressed to frons; epiphysis absent, fore leg fully developed, tibiae spined, spurs 0-2-2, tarsal claws bifid; fore wing (Fig. 41.65D) usually lacking at least 1 branch of R, 1 anal vein; hind wing with humeral vein present, vestigial, or absent, Sc+R<sub>1</sub> diverging from Rs at base, 2 anal veins, wing scales containing pterin pigments. Egg vertically fusiform, with vertical and horizontal ribs; laid singly or in groups. Larva (Fig. 41.66E) cylindrical, with numerous short, fine, secondary setae; crochets bi- or triordinal; sometimes gregarious. Pupa (Fig. 41.66F) angular, often with spines or ridges; attached by cremaster and central silken girdle.

The family includes 4 subfamilies: Pseudopontiinae, Dismorphiinae, Pierinae and Coliadinae, of which the last 2 occur in Australia.



COLIADINAE have the humeral vein in the hind wing greatly reduced or absent and, in Australia, larvae that usually feed on legumes (Caesalpiniaceae, Fabaceae and Mimosaceae), but also on Euphorbiaceae. *Catopsilia* (4 spp.) includes tropical, migratory species which also occur in the Oriental region. The larvae feed on *Cassia*. The white *C. pyranthe* and the lemon-yellow *C. pomona* occur in two forms, one with black antennae and the other with pink. *Eurema* (7 spp.) contains much smaller, usually sulphur-yellow species, which fly close to the ground. The larvae of *E. smilax*, found throughout the continent, feed on *Cassia* and *Neptunia*, whereas those of *E. hecabe* (Fig. 41.64C) are found mostly on *Indigofera*, *Sesbania*, *Acacia* and *Cassia*, as well as *Breynia* (Euphorbiaceae).

PIERINAE have the humeral vein long in the hind wing and larvae which feed mainly on Brassicaceae, Caparidaceae, Loranthaceae, Euphorbiaceae and Santalaceae. *Delias* (8 spp.) has bright, red and yellow markings beneath the wings. The larvae are dark with fine, whitish setae, and feed on mistletoes. Those of *D. harpalyce* are gregarious, and many of the shining, black, spiny pupae are attached to a communal web spun among foliage. *D. aganippe* (Fig. 41.64D) occurs in the south-west and the south-east, and *D. nigrina* is found from Cape York to southern N.S.W. The larvae of *Anaphaeis java* defoliate *Capparis* and *Apophyllum*, and the adults often take part in great migratory flights. *Elodina* (4 spp.) contains smaller species seldom recorded as far south as Sydney, N.S.W. Their larvae also feed on *Capparis*. *Pieris rapae* was introduced accidentally in 1937, and occurs commonly in eastern, southern and western mainland Australia and Tas. and locally in the interior and north; the larva damages crucifers.

**67. Nymphalidae** (Plate 8, G; Figs 41.64E–I). Small to large; most antennal segments with 2 ventral grooves; maxillary palps 1-segmented; labial palps ascending; epiphysis absent, male fore legs lack pretarsus, with fewer than 5 tarsomeres, lack tarsal spines, and covered with long scales; female fore legs reduced in size and not used for walking (except female *Libythea*); spurs 0-2-2 or 0-0-0; fore wing (Fig. 41.65E) with all branches of R present, 1A+2A simple or forming a basal fork; hind wing with humeral vein usually present, Sc+R<sub>1</sub> diverging from Rs near base, 2 anal veins. Egg taller than diameter, with vertical and horizontal ribs, or nearly spherical and sometimes nearly smooth. Larva with long, paired filaments (Fig. 41.66G), branching spines, or with fine, secondary setae and bifid anal segment or horned head; crochets multiordinal. Pupa (Fig. 41.66H) suspended by cremaster or, rarely, loose on ground beneath debris.

The Nymphalidae are characterised in both sexes by the tricarinate antenna and the elongate chaetosemata being parallel to the eye margin; the legs are described above. Ackery (1984) records 13 subfamilies of which 8 occur in Australia.

DANAINAE (milkweed butterflies) include large, conspicuous forms distasteful to birds and other predators. They are tenacious of life, and can survive physical injury of an order fatal to other Papilionoidea. The female fore tarsus is 4-segmented and strongly clubbed. Alar scent

glands and expandable, abdominal hair-pencils are present in the males. The larvae have 2 or more long, fleshy, dorsal filaments, and are usually aposematically marked with bright, transverse bands. They usually feed on Apocynaceae, Asclepiadaceae and Moraceae. The smooth pupae often have brilliantly reflective colours. The subfamily has been the subject of important phylogenetic studies (Ackery and Vane-Wright 1984; Kitching 1985). The large migratory *Danaus plexippus plexippus* was first seen in numbers in Australia about 1870, and now occurs wherever its introduced milkweed host plants, *Asclepias* and *Gomphocarpus*, are established. Its extensive two-way migrations and gregarious hibernation in North America are not a feature of its ecology here, although winter aggregations do occur in N.S.W. and S.A. *D. chrysippus* (Fig. 41.64E) is a smaller native species found throughout the continent. *Euploea* (10 spp.) is mainly tropical, but *E. core* extends south to Vic.; its larva feeds on *Ficus* (Moraceae), *Mandevilla*, oleander (Apocynaceae) and several Asclepiadaceae; the pupa is brilliantly patterned in silver or gold.

TELLERVINAE usually have yellow eyes in life; females with 5-segmented and not strongly clubbed fore tarsus. The larvae have a single pair of long, dorsal filaments on the metathorax. The subfamily contains only *Tellervo* (previously included in the Ithomiinae), with 6 black and white species (Ackery 1987). Only *T. zoilus* occurs in Australia, where it is restricted to rainforests in north-eastern Qld; the larvae feed on *Parsonia velutina* (Apocynaceae).

SATYRINAE include endemic genera in the south and a few Oriental genera in the north. The larvae feed on grasses or sedges; they have a bifid anal segment and often a pair of horns on the head. The adults are usually orange and black, with eye-spots, and the bases of the veins are often swollen. *Melanitis leda* is mainly crepuscular in habits; the larvae feed on *Imperata* and even sugar cane. *Hypocysta* (6 spp.) contains small, grass-frequenting species. Endemic genera include *Heteronympha* (7 spp.) and *Oreixenica* (6 spp.). *H. merope*, the common brown, is a ubiquitous species in the south-east and south-west. The most remarkable satyrine is *Tisiphone abeona* (Fig. 41.64F) in which several geographical forms occur between southern Qld and S.A.; its larvae feed on *Gahnia*.

AMATHUSIINAE lack swollen veins in the fore wing, usually have the hind wing cell open and, as in the Satyrinae, have prominent eye-spots on the wings, and larvae with forked posterior end; the larvae sometimes have the head armed and feed on Arecaceae, Musaceae, Poaceae and Smilacaceae. This Indo-Australian subfamily contains mainly large species. The only Australian representatives are 2 species of *Taenaris* known only from the Torres Strait islands.

CHARAXINAE are large and robust, lack swollen veins in the fore wing and usually have the hind wing cell open; the larvae usually have 1 or 2 pairs of prominent horns on the head, a pair of short terminal projections and setae restricted to the prolegs. Only 2 species occur in Australia. *Polyura sempronius* (Fig. 41.64G) is found in

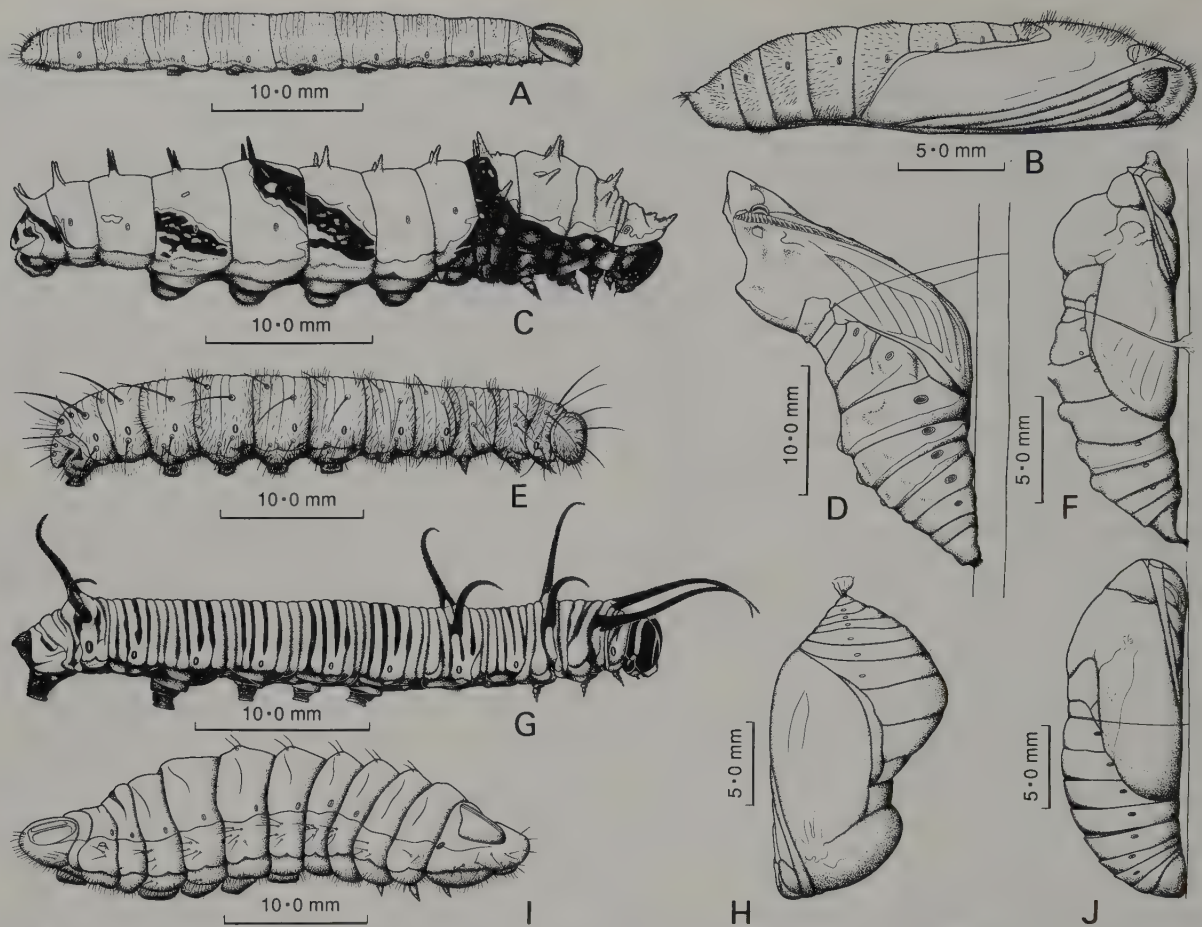


Fig. 41.66 Larvae and pupae of Hesperioidea and Papilionoidea: A, B, *Cephrenes*, Hesperidae; C, D, *Papilio*, Papilionidae; E, F, *Delias*, Pieridae; G, H, *Euploea*, Nymphalidae; I, J, *Ogyris*, Lycaenidae. [J. Wedgbrow]

north-western, northern and eastern Australia as far west as Adelaide, S.A. The adults fly rapidly and feed on fermenting juices; the larvae have 4 horns on the head and feed on many trees, including *Acacia*. *Charaxes latona* is known only from Cape York Peninsula.

NYPHALINAE are probably not monophyletic; the adults have symmetrical tarsal claws, have the cells of both fore and hind wing usually not closed by a tubular vein, and the females lack a scent-organ between abdominal segments 8 and 9; the larvae sometimes have branched spines. Those of the common migratory *Vanessa kershawi* (Fig. 41.64H) feed on Asteraceae, and those of *V. itea* on nettles. The subfamily contains many fine, tropical species, such as the red and black *Cethosia cydippe* (Plate 8, G). *Hypolimnias* (4 spp.) is also northern. The female of *H. misippus* resembles *Danaus chrysippus*, a species distasteful to birds, and may thereby derive some protection.

ACRAEINAE have usually asymmetrical, toothed claws in the males and the hind wing cell is closed by a tubular vein; the larvae have 6 longitudinal rows of often branched spines and a simple anal segment. *Acraea andromacha* from northern and eastern Australia is the only Australian species; the larvae feed mainly on *Passiflora* and *Adenia*.

LIBYTHEINAE have long, beak-like labial palps, fore legs not reduced in female, fore wing with apex produced and truncate and with 1A+2A forked; the larvae lack head ornamentation, have abundant short secondary setae; a bifid anal segment, and feed on Ulmaceae. This cosmopolitan subfamily contains only 10 species, with one in Australia, *Libythea geoffroy* (Fig. 41.64I) found in northern W.A., the N.T. and north-eastern Qld.

**68. Lycaenidae** (Plate 8, C, E; Figs 41.64J–L). Small to large; eyes often emarginate at base of antenna, or contiguous with antennal socket, often hairy; maxillary palps absent; labial palps ascending; epiphysis absent, fore leg in male somewhat reduced in most groups, normal in female, spurs 0-2-2, 0-1-1 or 0-0-0; fore wing (Fig. 41.65F) often lacking 1 or 2 branches of R, 1A+2A sometimes forked; hind wing with Sc+R<sub>1</sub> diverging from Rs near base, usually with 2 anal veins, margin often produced into 1 or more tails. Egg with diameter usually greater than height, or nearly spherical, often densely pitted or with projections. Larva (Fig. 41.66I) usually onisciform (i.e. shaped like a wood-louse), usually with retractile head, sometimes with dense, short hairs; abdomen often with medial dorsal gland on segment 7 and pair of dorsolateral, eversible organs on 8; prolegs with median, fleshy lobe, more or less interrupting the



uni- to multi-ordinal row of crochets; frequently associated with ants. Pupa (Fig. 41.66j) usually attached at anal end and by central, silken girdle; sometimes lying loose, cremaster absent.

The subfamilies Lipteninae, Poritiinae, Miletinae, Lycaeninae and Curetinae are not found in Australia; however, Lycaeninae are found both in New Guinea and New Zealand (Gibbs 1980).

LIPHYRINAE have the proboscis reduced and are represented by the large, crepuscular, orange and black *Liphyra brassolis* (Fig. 41.64L) from the north. The larva is found in the arboreal nests of *Oecophylla*, where it feeds on the ant larvae and pupae. It has a tough, leathery integument which can resist any attack from the ants and within which it pupates.

THECLINAE are one of the largest Australian subfamilies. The antennal club is cylindrical, the fore wing may lack 1 or 2 branches of R, the male scent scales are gathered in compact bands, often with hair brushes, and hind wings may bear 1 or 2 slender tails. The wings are usually some shade of blue, but are sometimes orange. The larvae are usually attended by ants, their dorsal glands secreting a substance sought by a single or at most a few species of ants. Several tropical species, such as *Hypolycaena phorbas* are attended by *Oecophylla*. The larvae of *Jalmenus* (9 spp.) feed openly during the day on foliage of *Acacia*. Those of the pale blue *J. evagoras* (Fig. 41.64k) are each attended by many small, black *Iridomyrmex*; they pupate gregariously on a communal web spun among the twigs. *Ogyris* (12 spp.) contains brilliant blue or purple species with larvae feeding on mistletoes. The nocturnal larvae hide during the day under bark, in holes or crevices, or in the attendant ant nests. The larvae and pupae of *O. genoveva* (Plate 8, E) occur in *Camponotus* nests at the foot of a eucalypt infested with mistletoe. *Hypochrysops* (18 spp.) have shining purple, blue or orange wings, with metallic green and red markings beneath (Sands 1986). The larvae of the purple *H. ignita* feed on *Acacia* and several other trees, while those of the orange *H. apelles* (Plate 8, C) feed on mangroves. *Paralucia* (Fig. 41.64j; 3 spp.) larvae feed at night on *Bursaria*, hiding during the day in ant nests at the base of the food plant.

POLYOMMATINAE, the other large Australian subfamily, usually have the antennal club more or less flattened, there is one R vein missing in the fore wing and R<sub>5</sub> and M<sub>1</sub> are separate at their origins, the male scent scales are usually spread over the wing surface in alternate rows with ordinary scales and the hind wings often have a slender tail. *Candalides* (12 spp.) have white to pale grey undersides and are tail-less; the larvae of some are ant

attended, while those of *C. absimilis* sometimes attack the young foliage of *Macadamia*, but also feed on several other plants. *Nacaduba* (4 spp.) and related genera usually have a tail, but *N. biocellata*, found throughout mainland Australia, is without a tail; its larvae feed on *Acacia* flowers. The small *Neolucia* (3 spp.) fly close to the ground near their food plants. The larva of *N. agricola*, brown with chequered wing margins, feeds in spring on flowers of Fabaceae. The ubiquitous *Zizina labradus* also feeds on Fabaceae, including lucerne and French beans.

RIODININAE have fore legs as in Nymphalidae, a single, ventral, medial patch of sensilla on the female pretarsus, and lack posterior apophyses in females. The only Australian species, *Praetaxila segecia* flies near the ground in rainforest on Cape York Peninsula; the early stages are unknown. [Harvey 1987]

### Superfamily BOMBYCOIDEA

Medium sized to large; ocelli and chaetosemata absent; antennae bipectinate, at least in male; maxillary palps small or absent; wings broad; body stout, clothed with long hair-scales; tympanal organs absent. Egg of flat type, smooth. Larva with dense secondary setae, usually on verrucae, or with sparse setae, or *scoli* (fleshy processes bearing secondary setae), often with dorsal projection on abdominal segment 8, crochets usually biordinal in a mesoseries; feeding exposed in daytime. Pupa stout, usually in cocoon of silk sometimes mixed with larval hairs; not protruded at ecdysis.

Broad wings and usually strongly pectinate antennae are features of the superfamily, which also displays a progressive reduction or loss of many characters found elsewhere. Ocelli, chaetosemata and tympanal organs are never present. The frenulum and retinaculum have been lost in Lasiocampidae, in the females of Anthelidae and some Eupterotidae, and in Saturniidae, but the humeral area of the hind wing is often expanded, permitting amplexiform wing-coupling. The proboscis is rudimentary or lost in all but a few of the least specialised Anthelidae, Eupterotidae and Saturniidae, and in the Carthaeidae. The larvae of Anthelidae, Eupterotidae and many Lasiocampidae have long, dense, secondary setae, unlike Bombycidae, Carthaeidae and Saturniidae, many of which have a caudal horn, sometimes only in the early instars, which suggests that the Sphingidae are indeed closely related to this group of families. Most species spin strong silken cocoons, and the silk spun by the commercial silkworm, *Bombyx mori*, and some Saturniidae has long been exploited by humans.

#### Key to the Families of Bombycoidea Known in Australia

1. Wings vestigial (♀♀ only) ..... Anthelidae (pt, p. 900)
- Fully winged ..... 2
- 2(1). M<sub>2</sub> arising nearer to M<sub>3</sub> than to M<sub>1</sub> in both pairs of wings ..... 3
- M<sub>2</sub> not arising nearer to M<sub>3</sub> than to M<sub>1</sub> in both pairs of wings ..... 4
- 3(2). Frenulum and retinaculum present in ♂, absent in ♀; fore wing with 1 or 2 areoles; Sc in hind wing without short costal branches ..... Anthelidae (pt, p. 900)
- Frenulum and retinaculum absent in both sexes; fore wing without areole; Sc in hind wing with 1 or more short costal branches ..... Lasiocampidae (p. 900)

- 4(2). Hind wing with 1 anal vein, humeral angle not thickened, frenulum absent; R in fore wing with 3 branches ..... **Saturniidae** (p. 903)  
 Hind wing with 2 anal veins, humeral angle with thickened frenulum base, frenulum often present; R in fore wing with 4 or 5 branches ..... 5
- 5(4). Both pairs of wings with prominent eye-spots ..... **Carthaeidae** (p. 902)  
 Wings without eye-spots ..... 6
- 6(5). Fore wing with  $R_1$ ,  $R_2$  and  $R_3$  separate and at least  $R_2$  and  $R_3$  arising successively from stem of  $R_{4+5}$  ..... **Bombycidae** (p. 902)  
 Fore wing with  $R_2$  and  $R_3$  stalked or fused and arising from  $R_4$  beyond its junction with  $R_5$  ..... **Eupterotidae** (p. 900)

**69. Lasiocampidae** (Figs 41.67A, B). Antennae bipectinate in both sexes; proboscis and maxillary palps absent; labial palps porrect, often beak-like with chaetosema-like sense organ on basal segment; epiphysis present in male, reduced or absent in female, tibial spurs very short, 0-2-2; fore wing (Fig. 41.68A) without retinaculum,  $R_2$  and  $R_3$  stalked, without areole; hind wing without frenulum, humeral angle expanded, Sc fused with  $R_s$  near base, or connected to  $R_s$  by  $R_1$ , Sc with 1 or more short branches to costa, CuP absent, 2 anal veins. Larva sometimes with dorsal protuberances, usually with dense secondary setae, sometimes on verrucae, or in pencils or tufts, setae never branched, sometimes scale-like, crochets biordinal, simple. Pupa often hairy, epicranial suture present, sometimes with hooked anal setae; in stiff silken cocoon.

The family is world-wide in distribution, but absent from New Zealand. The moths are stout bodied, hairy and sexually dimorphic, with fast-flying males and larger sluggish females. The larvae lie along twigs, to which they appress their dense, lateral hairs, effectively disguising their presence. The white, parchment-like cocoons are often spun among the foliage of the food plant.

*Pernattia* (3 spp.), the only Australian genus in the GASTROPACHINAE, has short labial palps, hairy eyes, and a broad 'sub-costal' cell in the hind wing, formed by  $R_1$  joining Sc and  $R_s$  beyond the end of the cell. The larva of *P. pusilla* feeds on *Casuarina*, spinning its white cocoon between branchlets.

All other Australian genera belong to the LASIOCAMPINAE, which have the valvae much reduced. *Entometa* (8 spp.) contains the largest species, with smooth eyes, long and beak-like labial palps, and Sc in the hind wing fused with  $R_s$  near its base. The dark larvae usually have a prominent projection on abdominal segment 8 and a pair of erectile, dorsal protuberances on the metathorax; they feed on *Eucalyptus*. *E. guttularis* (Fig. 41.67B) is found in much of mainland Australia. In *Genduara* (= *Crexa*) (11 spp.) the males have largely hyaline wings, whereas in *Pinara* (4 spp.) they are dark brown with an orange patch on the hind wing. The larvae of *G. acedesta* feed on mistletoe and *Exocarpos*, and those of *P. divisa* (Fig. 41.67A) on *Eucalyptus*.

**70. Anthelidae** (Figs 41.67C-G). Antennae bipectinate to apex in male, usually bipectinate or pectinate in female; proboscis rarely present; maxillary palps vestigial; labial palps porrect; epiphysis present in male, reduced or absent in female, tibial spurs short, 0-2-4 or 0-2-2; females rarely with vestigial wings; fore wing (Fig. 41.68B) with retinaculum in male, 1 or 2 areoles usually present,  $M_2$  arising nearer to  $M_3$  than to  $M_1$ , CuP absent,

$1A+2A$  forming basal fork; hind wing with functional frenulum in male, in female with only thickened frenulum base, Sc+ $R_1$  separate from  $R_s$ , or Sc connected to  $R_s$  by  $R_1$ ,  $M_2$  as in fore wing, CuP absent, 2 anal veins. Larva usually with verrucae and dense, branched or roughened setae, verrucae of abdominal segment 1 arranged differently from those of 2-8; crochets biordinal or multiordinal, simple. Pupa in double-walled cocoon of silk often mixed with larval hairs.

The family (Turner 1921) forms a conspicuous element of the Australian fauna, but elsewhere is known only from New Guinea.

Adult MUNYCHRYIINAE have a proboscis; the larvae have small, scattered, spatulate secondary setae, lack verrucae and have hypertrophied prothoracic legs and posteriorly expanded anal prolegs. *Munychryia* (Fig. 41.67C; 2 spp.) occurs from North Qld to W.A.; the longitudinally striped larvae feed on *Casuarina*. *Gephyroneura* (1 sp.) is restricted to North Qld. [Common and McFarland 1970]

ANTHELINAE lack the proboscis and have the larval secondary setae on well defined verrucae. *Chelepteryx* (2 spp.), which has medial spurs on the hind tibiae, includes the large *C. collesi* (Fig. 41.67G), females of which reach 18 cm in wing-span. The *Eucalyptus*-feeding larvae are covered with tufts of stout setae, which are thrust through the silk fusiform cocoon during its construction. If the larvae or cocoons are handled, these bristles readily enter the skin and cause mechanical irritation. *Anthela* (51 spp.) lacks median spurs on the hind tibiae. Some of the species are extremely variable in colour and pattern, especially in the male. Thus in *A. nicotiae* the males may be brown, yellow or red, and in *A. excellens* (Fig. 41.67E) they vary from yellowish green through yellow to bright orange-red. A heavily blotched form in this and other species is fairly common. *Acacia dealbata* is the normal food plant of *A. nicotiae*, but at times both it and *A. excellens* damage *Pinus radiata*. In *Chenuala* (1 sp.) the frenulum is reduced in the male, and the tornus of the hind wing is produced. *C. heliaspis* (Fig. 41.67F) is sexually dimorphic, with reddish brown male and larger pale grey female. The larva feeds on *Eucalyptus*, but also attacks *Pinus radiata*. In *Pterolocera* (Fig. 41.67D), with 4 named and many unnamed species, the male antennae have very long pectinations, whereas the female antennae are filiform. It is the only genus in which the females usually have vestigial wings; the strong legs have rudimentary tibial spurs. *Pterolocera* larvae often feed on grasses, and spin a flask-shaped cocoon in a vertical shaft in the soil, with the emergence exit just below the surface.

**71. Eupterotidae** (Figs 41.67H, I). Antennae bipecti-



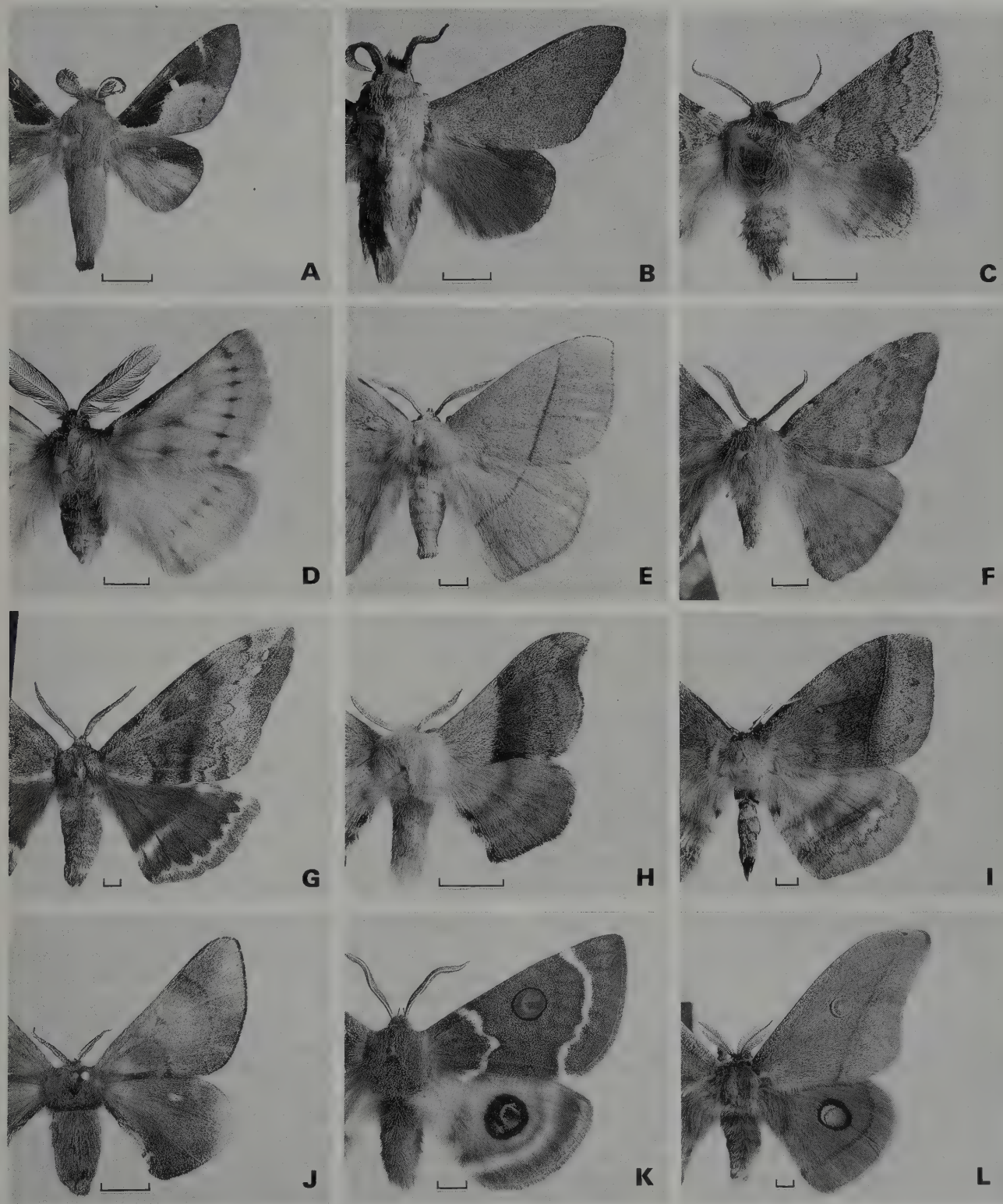


Fig. 41.67 A, *Pinara divisa*, B, *Entometa guttularis*, Lasiocampidae; C, *Munychryia senicula*, D, *Pterolocera* sp., E, *Anthela excellens*, F, *Chenuala heliaspis*, G, *Chelepteryx collesi*, Anthelidae; H, *Panacela lewinae*, I, *Eupterote expansa*, Eupterotidae; J, *Gastriodiota adoxima*, Bombycidae; K, *Carthaea saturnioides*, Carthaeidae; L, *Opodipthera helena*, Saturniidae. Scales = 5 mm.

[J. Green, C. Lourandos]

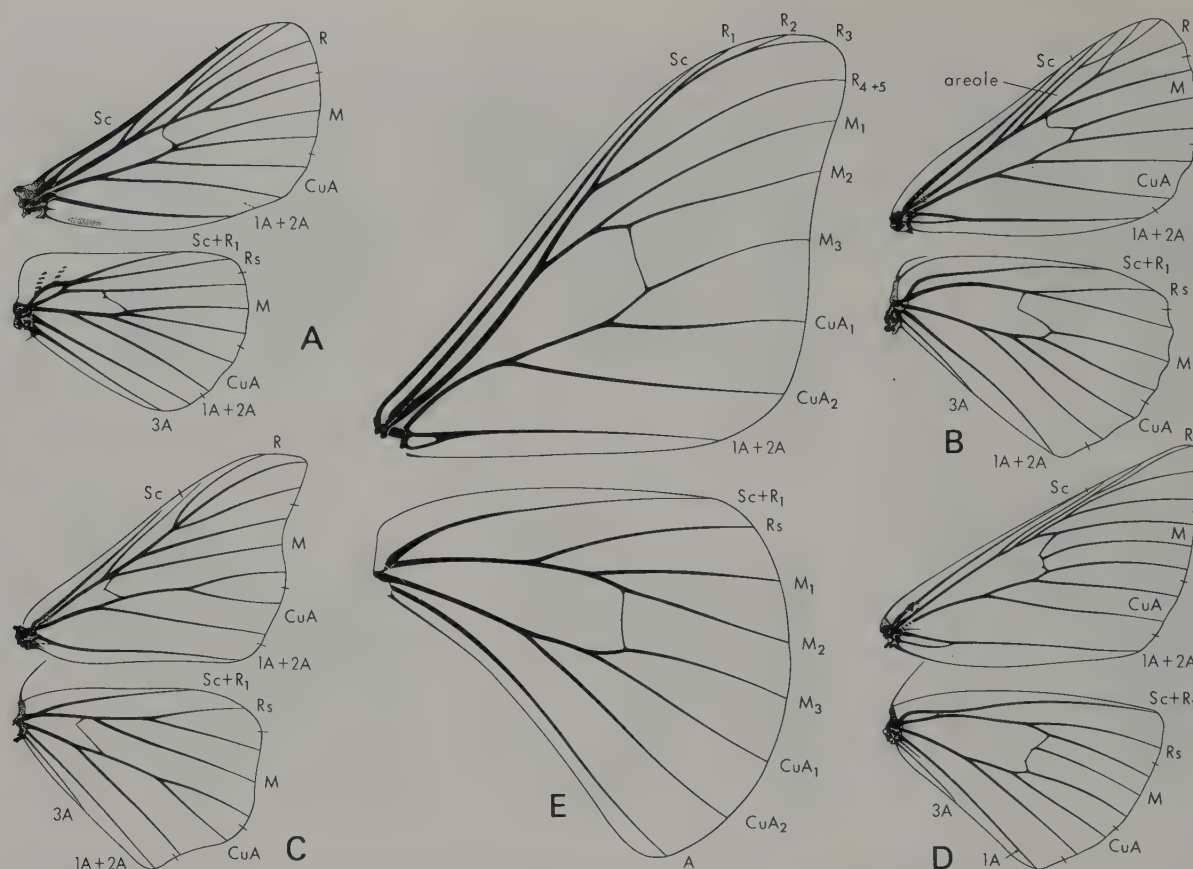


Fig. 41.68 Wing venation of Bombycoidea: A, *Porela*, Lasiocampidae; B, *Anthela*, Anthelidae; C, *Panacela*, Eupterotidae; D, *Carthaea*, Carthaeidae; E, *Opodiphthera*, Saturniidae. [J. Wedgbrow]

nate to apex in both sexes; proboscis very weak or absent; maxillary palps absent; labial palps short; epiphysis sometimes present, tibial spurs 0-2-2; fore wing (Fig. 41.68C) usually with retinaculum, areole absent,  $R_2$  and  $R_3$  usually fused, and  $R_2$  or  $R_{2+3}$  arising from  $R_4$  beyond its junction with  $R_5$ , CuP vestigial or absent; hind wing with frenulum usually present, functional, Sc and Rs well separated, usually connected by  $R_1$ , CuP vestigial or absent, 2 anal veins. Larva with dense secondary setae, often branched, dorsal verrucae of abdominal segment 1 similar to those of 2-8, crochets biordinal, shorter series with subapical spur or dentate. Pupa in flimsy cocoon of silk mixed with larval hairs.

This chiefly Old World family (Forbes 1955) includes 3 genera in Australia. In the Indo-Malayan *Eupterote* (1 sp.) and in *Cotana* (2 spp.) which also occurs in New Guinea, a large epiphysis is present in the male, but absent in the female. *Eupterote* lacks the frenulum and retinaculum found in *Cotana*. *E. expansa* (Fig. 41.67I) is a large, anthelid-like species from northern Qld. *Panacela* (4 spp.) is endemic and has a frenulum and retinaculum in males, but not in females; it is without an epiphysis and the tornus of the hind wing is slightly produced. The larvae of *P. lewinae* (Fig. 41.67H) live gregariously in communal shelters of silk, spun in the branches of *Exocarpos*, *Eucalyptus* and other trees, and sometimes cause extensive defoliation. They occasionally damage

*Pinus radiata*. The larval hairs are capable of inflicting skin rashes in humans.

**72. Bombycidae** (Fig. 41.67J). Antenna bipectinate to apex in both sexes; proboscis absent; maxillary palps absent; labial palps short; epiphysis present or absent; spurs 0-2-2 or 0-0-0; fore wing with or without retinaculum,  $R_1$ ,  $R_2$  and  $R_3$  separate and at least  $R_2$  and  $R_3$  arising successively from stem of  $R_{4+5}$ , CuP sometimes present; hind wing with functional or reduced frenulum present, dorsum often pleated, somewhat concave, Sc and Rs usually connected by  $R_1$ , CuP often present towards margin. Larva with coarse, secondary setae in early instars, with fine secondary setae (in *Bombyx*) or scattered, short, coarse secondary setae (in *Gastridiota*) when mature; crochets biordinal, simple. Pupa in dense cocoon of silk.

Apart from the introduced, domesticated, commercial silkworm, *Bombyx mori*, the most important silk-producing moth, which has so-called 'naked' larvae because the secondary setae are extremely fine, 2 native, Australian species probably belong to this family. *Gastridiota adoxima* (Fig. 41.67J) is known from rainforests in southern Qld and northern N.S.W.; the larvae, which have scattered, very short setae and bright yellow spiracles, feed on *Ficus* and pupate in an elongate strong cocoon. One species of *Elachyophthalma* is known from Cape York Peninsula. [Common and Edwards 1991]

**73. Carthaeidae** (Fig. 41.67K). Antennae bipectinate



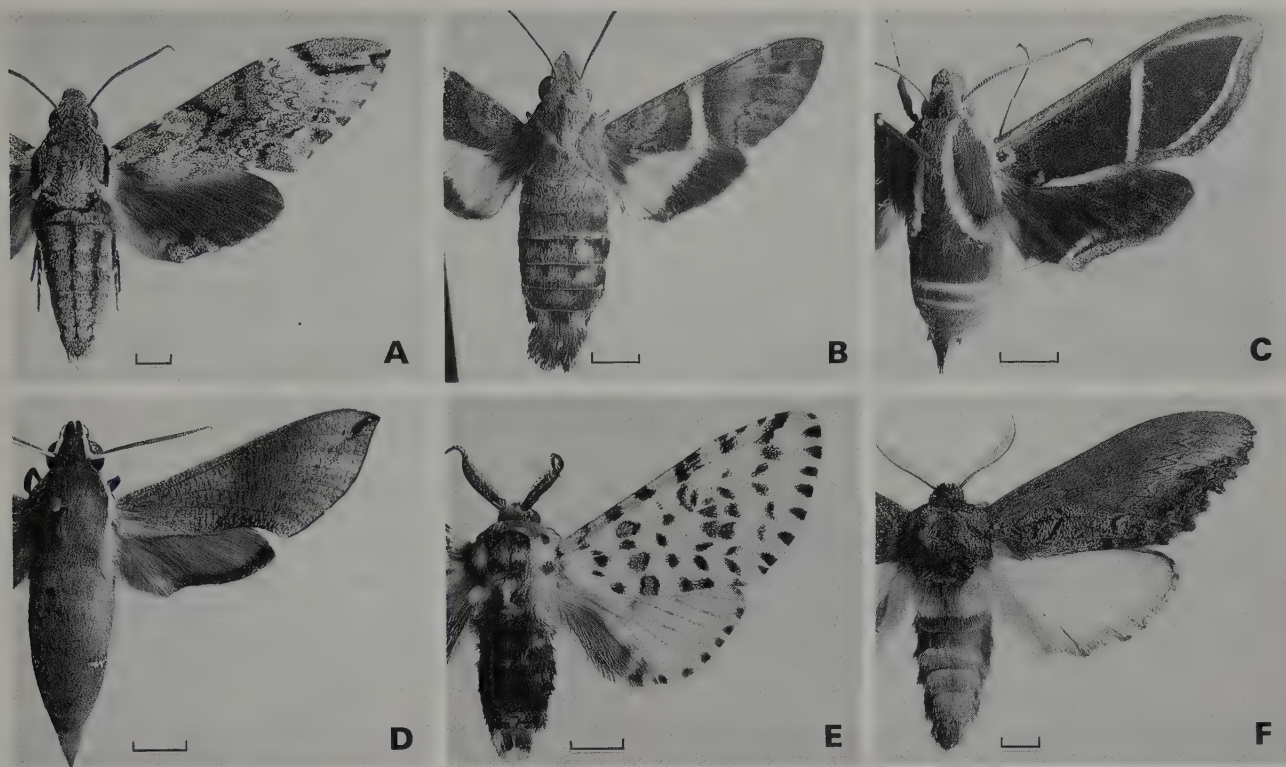


Fig. 41.69 A, *Psilogramma menephron*, B, *Macroglossum hirundo*, C, *Cizara ardenia*, D, *Hippotion scrofa*, Sphingidae; E, *Cerura australis*, F, *Hylaeora dilucida*, Notodontidae. Scales = 5 mm. [C. Lourandos]

to apex in male, dentate in female, flagellum scaled; proboscis strong; maxillary palps 3-segmented; labial palps strong, ascending; epiphysis present; tibial spurs 0-2-4, apices bare; fore wing (Fig. 41.68D) with retinaculum in male,  $R_2$  and  $R_3$  stalked,  $M_2$  arising about equidistant between  $M_1$  and  $M_3$ , CuP absent; hind wing with frenulum strong in male, about 10 short bristles in female, Sc approaching Rs before one-half of discal cell where  $R_1$  joins Rs and Sc,  $M_2$  as in fore wing, CuP absent, 1A and 3A present, 2A vestigial. Larva in early instars with scoli and dorsal horn on abdominal segment 8, mature larva (Fig. 41.71A) with minute secondary setae and with slight hump on segment 8, and prolegs massive, crochets biordinal, simple. Pupa with cremaster bearing a group of hooked setae; in flimsy cocoon on ground.

The single fine species, *Carthaea saturnioides* (Fig. 41.67K) from south-western Australia (Common 1966b), is grey with a rose-flushed hind wing. When disturbed suddenly, the insect displays its eye-spots by depressing the head, protracting the fore wings, and moving the hind wings rhythmically. The handsome, orange and brown larva, with lateral eye-spots, feeds exposed in the early summer on the young foliage of *Dryandra*, *Banksia* and *Grevillea* (Proteaceae).

**74. Saturniidae** (Attacidae) (Plate 8, F; Fig. 41.67L). Antennae short, naked, bipectinate to apex in both sexes, each segment usually with 4 pectinations; proboscis usu-

ally absent; maxillary palps vestigial; labial palps small; epiphysis present, tibial spurs 0-2-2, 0-2-4 or absent, short, apices bare; wings very broad; fore wing (Fig. 41.68E) often falcate, without retinaculum, areole absent, R usually with 3, never more than 4 branches,  $M_2$  arising nearer to  $M_1$  than to  $M_3$ , CuP absent; hind wing without frenulum or thickened frenulum base, humeral angle expanded, Sc+ $R_1$  diverging from Rs,  $M_2$  as in fore wing, CuP absent, 1 anal vein. Larva (Fig. 41.71B) with scoli, at least in early instars, secondary setae usually small, numerous, abdominal segment 8 often with dorsal projection, crochets biordinal, simple. Pupa with cremaster simple, when present; in tough silken cocoon.

The family (Michener 1952) includes some of the largest and finest moths, with stout, hairy bodies, small in proportion to the broad wings, and prominent eye-spots. Some Australian genera also occur in the Oriental or Papuan areas. *Attacus* (1 sp.) and *Coscinocera* (1 sp.) are without tibial spurs, and the discal cell is open in both wings. *A. wardi* occurs at Darwin, N.T., and in Indonesia. The tornal area of the hind wing in *C. hercules* (Plate 8, F), a striking species from northern Qld and New Guinea, is produced into a long tail, much broader in the female. In *Opodipthera* (8 spp.) an epiphysis is present in both sexes, and the mid and hind tibiae each has an apical pair of short stout spurs. The first axillary sclerite of the fore wing is armed with a strong distal hook, used by the



Fig. 41.70 Wing venation of *Hippotion*, Sphingidae. [J. Wedgbrow]

freshly emerged moth to open the cocoon. *O. eucalypti* is from eastern Australia, and *O. helena* (Fig. 41.67L) from both the south-east and south-west. The mature larva of *O. eucalypti* (Fig. 41.71B) is bluish green, with a pale lateral stripe and red and blue scoli; that of *O. helena* is green with a broad pink lateral stripe, and lacks scoli. Both feed on the foliage of *Eucalyptus*, and attach their oval, grey cocoons to the bark. The larvae of the larger *O. loranthei* feed gregariously on mistletoe growing on *Eucalyptus*; the cocoons are spun in a mass on the butt of the mistletoe.

### Superfamily SPHINGOIDEA

**75. Sphingidae** (Figs 41.69A–D). Large; ocelli and chaetosemata absent; antennae usually thickened, sometimes clavate or hooked apically, ciliate, serrate, or shortly pectinate in male, filiform in female; proboscis usually strong, often long; maxillary palps 1-segmented; labial palps thick, ascending, appressed to frons, with unscaled areas on inner surface, basal segment often with patch of sensory hairs on inner surface; epiphysis present, tibial spurs 0-2-4 or rarely 0-2-2; fore wing (Fig. 41.70) long, narrow, CuP absent, one other vein usually absent, 1A+2A forked at base, retinaculum rarely absent; hind wing much shorter than fore wing, with anal lobe, frenulum usually strong, Sc connected to Rs by  $R_1$  at middle of cell, Sc+ $R_1$  approaching Rs beyond cell, CuP absent, 2 anal veins; tympanal organs absent; abdomen large, fusiform, posterior margins of segments usually with flattened spines or stiff, modified scales. Egg of flat type. Larva (Fig. 41.71C) without conspicuous setae, abdominal segment 8 usually with spine-like dorsal horn, sometimes rudimentary in final instar, crochets biordinal, in a mesoseries, anal prolegs massive; feeding exposed in daytime. Pupa (Fig. 41.71D) fusiform, mouth-parts displaced anteriorly, cremaster prominent, rarely armed; in cell in soil, or in flimsy cocoon amongst detritus.

This mainly tropical family includes fast-flying species, often with long proboscis used for ingesting nectar as the insect hovers before flowers. Twenty-four genera occur in Australia, most of which are found also in

New Guinea and the Orient; a few species are almost cosmopolitan. The family has sometimes been referred to the Bombycoidea because of larval characters. Röttschild and Jordan (1903) recognised 5 subfamilies and Hodges (1971) 2 with 5 tribes; the latter view is accepted here. D'Abrera (1986) illustrated most species of the family.

SPHINGINAE lack short sensory setae on the naked, inner surface of the 1st segment of the labial palp, and have symmetrical male genitalia; larvae have a caudal horn but are usually without subdorsal eye-spots. Only 9 Australian species in 8 genera belong here. The large grey *Psilogramma menephron* (Fig. 41.69A) ranges from the eastern Palaearctic to Australia; the larvae feed on privet (*Ligustrum*) and jasmine but also on other plants, and the proboscis in the pupa is free (Fig. 41.71D). In the cosmopolitan *Agrius* (2 spp.), the pupal proboscis is also free, but distally recurved, whereas in the endemic *Coenotes* (1 sp.) it is fused to the body. *C. eremophila* occurs widely in the northern inland, where its larvae sometimes defoliate *Eremophila* and *Myoporum*.

MACROGLOSSINAE have short sensory setae on the naked, inner surface of the 1st segment of the labial palp, and male genitalia symmetrical or asymmetrical; larvae are sometimes without a caudal horn, and often have subdorsal eye-spots. The endemic *Metamimas* (1 sp.) and *Coequosa* (1 sp.) have a short, stout proboscis; the retinaculum is absent, the frenulum is vestigial, and in *Coequosa* the hind tibiae lack medial spurs. The mature larva of *C. triangularis*, which feeds mainly on *Persoonia* and *Banksia*, but also on *Macadamia*, *Grevillea* and *Stenocarpus*, lacks a caudal horn, but has a shining, black spot on each of the enormous anal claspers. *Cephonodes* (4 spp.) is day flying, with largely hyaline wings, clubbed and hooked antennae, and asymmetrical male genitalia. As they fly in sunshine with an expanded anal tuft of long hair-scales, they resemble large bumble bees. The larvae of *C. kingii* usually feed on *Canthium* or gardenia. *Gnathothlibus erotus* is found from India to Australia; the larvae, which feed on *Cayratia*, *Cissus* and other Vitaceae, have a strongly curved caudal horn and usually 8 small, subdorsal eye-spots. *Cizara ardenia* (Fig. 41.69C), with rich green fore wings, occurs along the east coast, where the larvae feed on Rubiaceae, including *Morinda* and *Coprosma*. *MacroGLOSSUM* (13 spp.) contains many Indo-Malayan and Papuan species (Moulds 1985). In flight they resemble bumble bees but, unlike *Cephonodes*, the wings are scaled and the abdomen bears lateral scale-tufts. *M. hirundo* (Fig. 41.69B), with orange hind wings, is found in the N.T. and eastern Australia as far south as Sydney, N.S.W. The larvae feed on Rubiaceae. The subfamily also includes widely distributed *Hyles* (1 sp.), *Hippotion* (5 spp.) and *Theretra* (11 spp.). *Hyles lineata* is common inland, with larvae feeding on *Boerhavia* and *Tribulus*. *Hippotion scrofa* (Fig. 41.69D) occurs throughout the mainland and Tas. where the larvae feed on Vitaceae, Onagraceae, Rubiaceae and other plants. *H. celerio* ranges with little variation over most of the Old World. The larva, with large eye-spots on abdominal segments 1 and 2, feeds on plants in several families and is a minor pest of grape vines. [Moulds 1984]



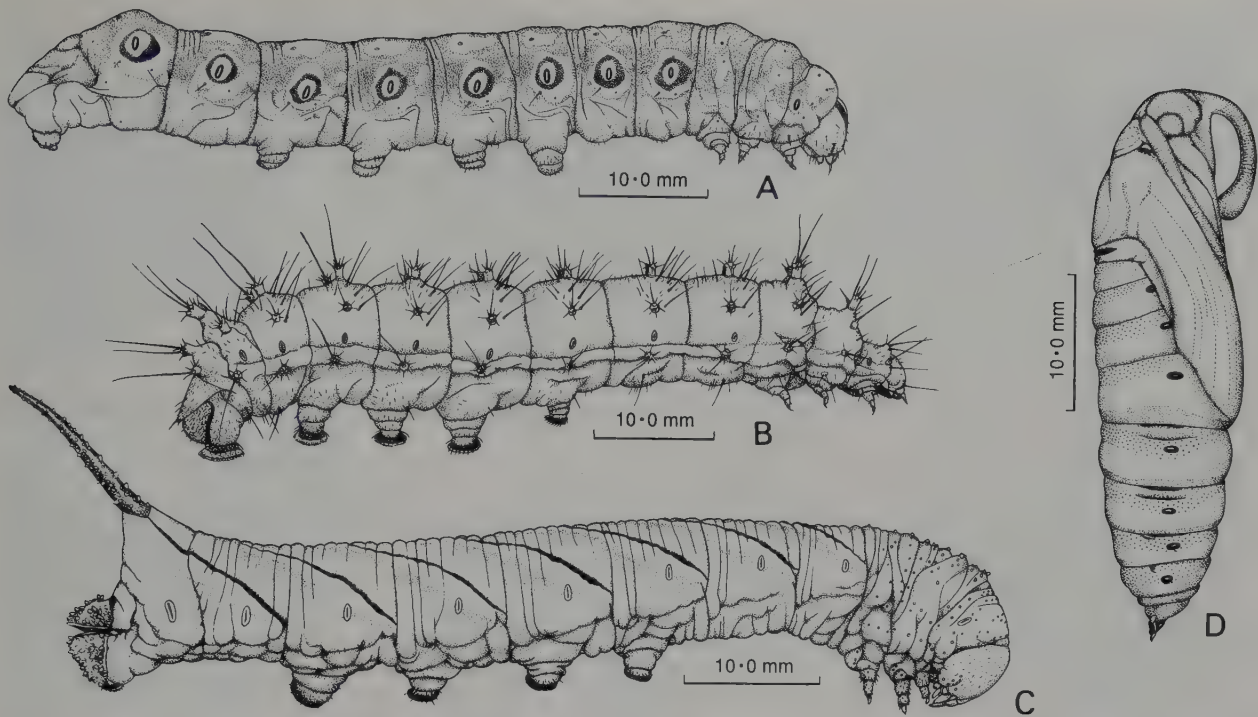


Fig. 41.71 Larvae and pupae of Bombycoidea and Sphingoidea: A, larva of *Carthaea*, Carthaeidae; B, larva of *Opodiphthera eucalypti*, Saturniidae; C, D, larva, pupa of *Psilogramma*, Sphingidae. [B. Rankin]

### Superfamily NOCTUOIDEA

Small to large; ocelli present or absent; chaetosemata absent; proboscis often strong, sometimes reduced or absent; maxillary palps very small, 1–4-segmented, or absent; fore wing without CuP; hind wing with frenulum, CuP absent, 1A+2A sometimes forming anal fork; metathorax with tympanal organs, rarely reduced or lost (*Amata*), tympanum directed ventrally or obliquely posteriorly; abdomen with basal counter-tympanal cavities, usually with prominent hood, with abdominal spiracle 1 either on anterior face (hood postspiracular) or at posteroventral angle (hood pre-spiracular). Eggs of upright type. Larva sometimes with dense secondary setae, crochets uniordinal, rarely biordinal (a few Noctuidae), in a mesoserries.

This large superfamily is united by the presence of

metathoracic tympanal organs; each organ usually has a large counter-tympanal cavity, with a projecting hood at the base of the abdomen. The tympanal organs are secondarily reduced in Ctenuchinae, female Lymantriidae and some Diopitidae. The superfamily contains 9 families of which the Diopitidae and Thyretidae do not occur in Australia. The Ctenuchinae, Nolinae and Agaristinae have sometimes been treated as separate families. The projecting hood is prespiracular in Lymantriidae, Arctiidae, Aganidae and Herminiidae and postspiracular in Notodontidae, Diopitidae, Thaumetopoeidae and Noctuidae. While each tympanal organ in Notodontidae and Thaumetopoeidae has a single acoustic sense cell, that in the remaining families has 2 (Roeder 1974). J. S. Miller (1989) indicated that the Notodontidae are paraphyletic with respect to the New World Diopitidae.

### Key to the Families of Noctuoidea Known in Australia

1. Fully winged ..... 4
- Abbreviated crumpled vestiges of wings (♀ ♀ only) ..... 11
- 2(1) Fore wing with  $M_2$  not arising nearer to  $M_3$  than to  $M_1$ ; tympanum directed ventrally, metascutum with blister-like bulla ..... 3
- Fore wing with  $M_2$ , when present, arising nearer to  $M_3$  than to  $M_1$ ; tympanum directed obliquely posteriorly, metascutum without blister-like bulla ..... 4
- 3(2). Proboscis usually present and coiled; maxillary palps minute, with maximum of 2 segments; abdominal tip without specialised vestiture ..... **Notodontidae** (p. 906)
- Proboscis usually vestigial or absent; if present, maxillary palps with 4 segments; abdominal tip usually with long pili-form scales in ♂, and dense bunch of deciduous scales in ♀ ..... **Thaumetopoeidae** (p. 906)
- 4(2). Hind wing with  $Sc+R_1$  coincident with  $R_s$  (i.e.  $Sc+R_1$  apparently absent); wasp-like species with boldly ringed abdomen ..... **Arctiidae-Ctenuchinae** (pt, p. 908)
- Hind wing with  $Sc$  only partly fused with  $R_s$  or  $R_1$  joining  $Sc$  and  $R_1$ ; species not wasp-like ..... 5
- 5(4). Hind wing with  $M_2$  arising nearer to  $M_3$  than to  $M_1$  ..... 6

- Hind wing with  $M_2$  not arising nearer to  $M_3$  than to  $M_1$  ..... 10
- 6(5). Hind wing with Sc sharply diverging from Rs at base and then fusing with Rs for a short distance near middle of discal cell, or connected to Rs by  $R_1$  towards middle of discal cell (Figs 41.76A, B) ..... 7
- Hind wing with Sc not sharply diverging from Rs at base, but either approximated to Rs near base and then fused with Rs for a short distance, or fused with Rs from base to near or beyond middle of discal cell (Figs 41.76C–G) ..... 8
- 7(6). Proboscis very weak or absent; ocelli absent; fore wing with 1A+2A not forming basal fork; ♀ abdomen with large, compact, terminal tuft ..... **Lymantriidae** (pt. p. 908)
- Proboscis strong; ocelli present; fore wing with 1A+2A forming basal fork; ♀ abdomen without terminal tuft ..... **Aganaiidae** (p. 910)
- 8(7). Hind wing with Sc+ $R_1$  approximated to Rs near base and then fused with Rs for a short distance, but not beyond one-third of discal cell; Sc+ $R_1$  not swollen near base (Fig. 41.76F) ..... **Noctuidae** (pt. p. 910)
- Hind wing with Sc+ $R_1$  fused with Rs from base to near or even beyond middle of discal cell; if Sc+ $R_1$  separate from, but approximated to, Rs near base and then fused with Rs to one-third of discal cell or less, then Sc+ $R_1$  swollen near base (Figs 41.76C–E, G) ..... 9
- 9(8). Hood of counter-tympanal cavity at base of abdomen postspiracular, i.e. spiracle deep within counter-tympanal cavity (Fig. 41.6A) ..... **Noctuidae** (pt. p. 910)
- Hood of counter-tympanal cavity at base of abdomen prespiracular, i.e. spiracle posterior to hood, or at or near its margin outside (Fig. 41.6B) ..... 10
- 10(9). Labial palps very large, either upcurved to beyond vertex or strongly extended in front of head; prothorax without defensive glands; coloration of vestiture cryptic ..... **Herminiidae** (p. 910)
- Labial palps short or fairly short, usually upturned but not to beyond vertex; prothorax with paired defensive glands; coloration of vestiture aposematic ..... **Arctiidae** (pt. p. 908)
- 11(3). Antennae simple; integument of abdomen and thorax whitish or pinkish, with distinct brownish black, dorsal pattern ... **Arctiidae** (pt. p. 908)
- Antennae with rudimentary pectination; integument not distinctly patterned ..... **Lymantriidae** (pt. p. 908)

**76. Notodontidae** (Figs 41.69E, F). Medium sized to large; ocelli absent; antennae usually bipectinate in male, filiform or bipectinate in female, scale tufts often raised on scape; proboscis strong, occasionally reduced or absent; maxillary palps very small, 2-segmented; labial palps porrect, ascending; epiphysis present in male, absent in female, spurs 0-2-4 or 0-2-2; fore wing (Fig. 41.73A) often with areole,  $M_2$  arising midway between  $M_1$  and  $M_3$ , 1A+2A sometimes forming small fork; hind wing with frenulum, Sc+ $R_1$  approximated to Rs, or Sc connected to Rs by  $R_1$ ,  $M_2$  as in fore wing, 2 anal veins; thorax often with dorsal scale-crests, metathoracic tympanal organs with tympanum directed ventrally; male abdomen sometimes with scaled flaps on S4. Eggs hemispherical or nearly spherical, of upright type. Larva (Fig. 41.77A) with spines, fleshy tubercles or humps, sometimes with secondary setae, prothorax sometimes with forked eversible organ beneath head producing secretions containing formic acid and ketones, anal prolegs often reduced or modified, usually with 4 pairs of ventral prolegs, crochets uniordinal in a mesoserries; external, arbor-eal feeders. Pupa (Fig. 41.77B) well sclerotised, thoracic dorsum sometimes and abdomen usually with punctures, cremaster usually present; in cell in soil or tough cocoon.

Both adults and larvae are structurally diverse and the monophyly of the family remains to be established firmly. It is possible that not only New World Dioptriidae but also the Thaumetopoeidae are subsets of the Notodontidae. However, notodontid larvae are often quite characteristic and the only lepidopterans known to produce ketones. The Australian fauna contains more than 30 genera. *Gallaba* (6 spp.), with a long scale-tuft on the frons and tegulae, occurs in southern Australia. *Cerura* (2 spp.) is a widely distributed genus in the Old World with brightly

coloured larvae with a pair of long posterior whiplash organs replacing the anal prolegs; *C. australis* (Fig. 41.69E) occurs in or near rainforest from central Qld to central eastern N.S.W., with larva on *Scolopia braunii*. *Danima banksiae* occurs widely; the larva, which feeds on *Banksia* and other Proteaceae, throws back its head when irritated (Fig. 41.77A) and displays a purple, bifid, prothoracic organ. The larva of *Neola semiaurata* feeds on *Acacia* and displays a large, normally hidden eye-spot on each side of abdominal segment 8 when disturbed; it occurs from central Qld to southern N.S.W. [Kiriakoff 1968; J. D. Holloway 1983]

**77. Thaumetopoeidae** (Figs 41.72A, B). Medium sized to large; head with piliform scales; ocelli vestigial or absent; antenna usually bipectinate to apex in both sexes, rarely lamellate in male and filiform in female; proboscis vestigial or absent, rarely well developed; maxillary palps 2–4-segmented or absent; labial palps very small or vestigial; epiphysis present in male, absent in female; spurs 0-2-4 or 0-2-2; metathoracic tympanal organs with tympanum directed ventrally, usually with metascutal blister-like bulla; fore wing (Fig. 41.73B) with  $R_1$  separated from remaining R-branches or absent,  $M_2$  arises about midway between  $M_1$  and  $M_3$ , 1A+2A may have small fork; hind wing Sc may approach Rs, be connected to Rs by  $R_1$ , be fused with Rs for a short distance or run close to Rs before or after middle, Rs and  $M_1$  stalked,  $M_2$  usually nearer  $M_1$  than  $M_3$ ; abdomen with long piliform scales, males usually with long scale tuft at tip, females of most genera with large, dense, anal tuft of deciduous, piliform scales. Egg usually globular with a flattened base; mixed with deciduous scales from tip of female abdomen. Larva with dense secondary setae, many on verrucae; hairs sometimes with barbs; anal prolegs not reduced; with 4



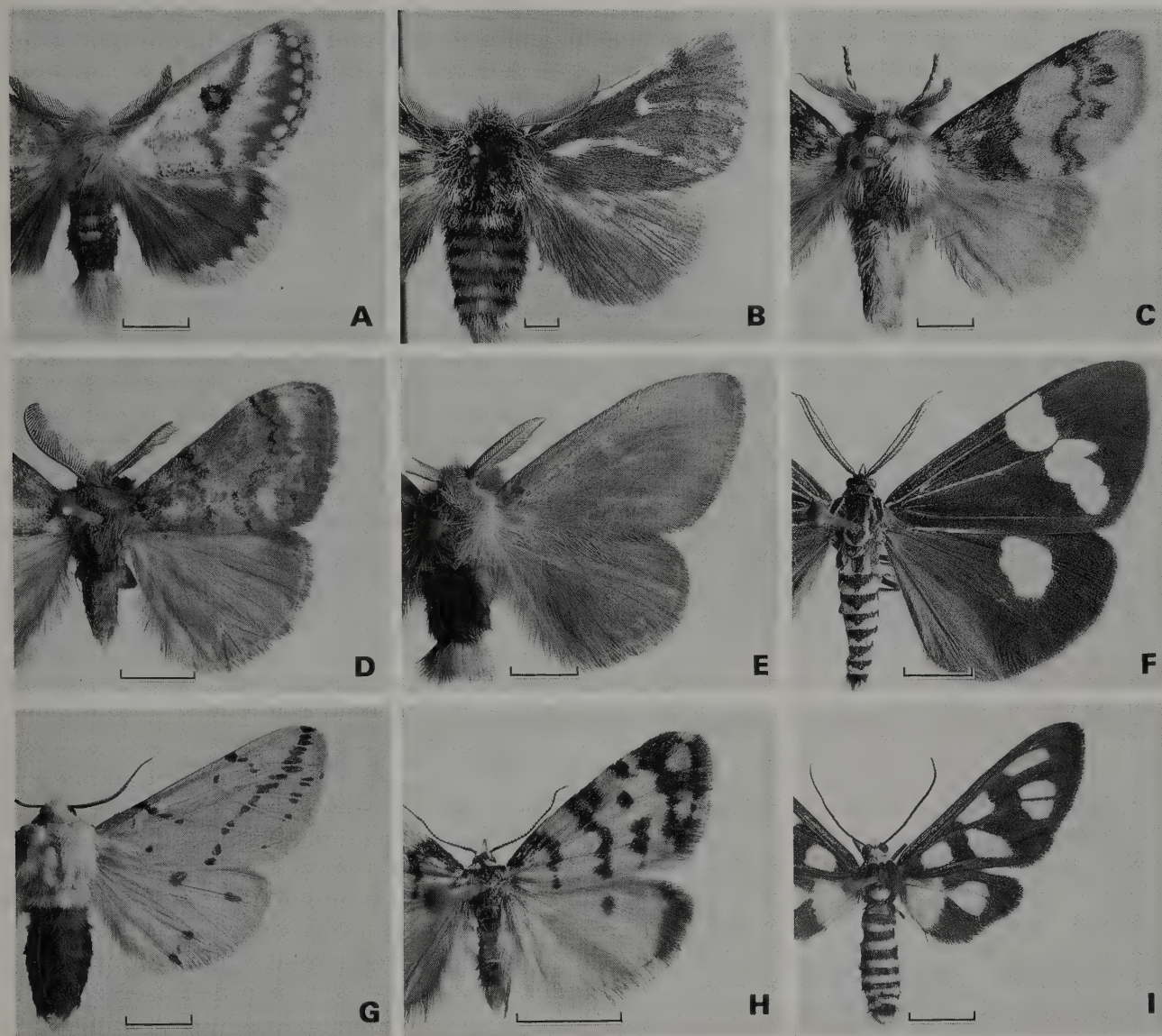


Fig. 41.72 A, *Epicoma melanosticta*, B, *Ochrogaster lunifer*, Thaumetopoeidae; C, *Iropoca rotundata*, D, *Teia athlophora*, E, *Euproctis edwardsii*, Lymantriidae; F, *Nyctemera amica*, G, *Spilosoma canescens*, H, *Thallarcha jocularis*, I, *Amata trigonophora*, Arctiidae. Scales = 3 mm.

[J. Green, C. Lourandos]

pairs of ventral prolegs with crochets usually in uniordinal mesoserries; exposed nocturnal feeders, often gregarious, living in silk bags and displaying processionary behaviour. Pupa (Fig. 41.77c) well sclerotised, with ventrally bent cremaster with apical pair of diverging spines; in flimsy cocoon in soil.

This is a relatively small Old World family which perhaps is best known for its usually colonial, often processionary, hairy larvae which often form silken nests for shelter and may cause serious defoliation of the host trees; the larval hairs sometimes cause skin rashes in humans. Species of *Diceratucha* are small and noline-like; the larvae are unknown but the adults are similar to those of *Discophlebia* (6 spp.) in wing-pattern, presence

of 4-segmented maxillary palps and proboscis and absence of female abdominal hair tuft; the larvae of *D. catocalina* have sparse secondary setae, feed on *Eucalyptus* and show some gregarious behaviour when young. *Oenosandra boisduvalii* is sexually dimorphic and widely distributed; the male has bipectinate and the female fili-form antennae; the adults have a small proboscis and well developed, terminal hair tufts; the larvae lack dense secondary setae and have biordinal crochets; they shelter beneath loose bark of *Eucalyptus*, feeding at night on the foliage. *Ochrogaster lunifer* (Fig. 41.72b) has gregarious larvae living in large silk bags, partly filled with excrement and cast skins, spun among the branches of *Acacia* and other trees; at night they move in processions to feed,



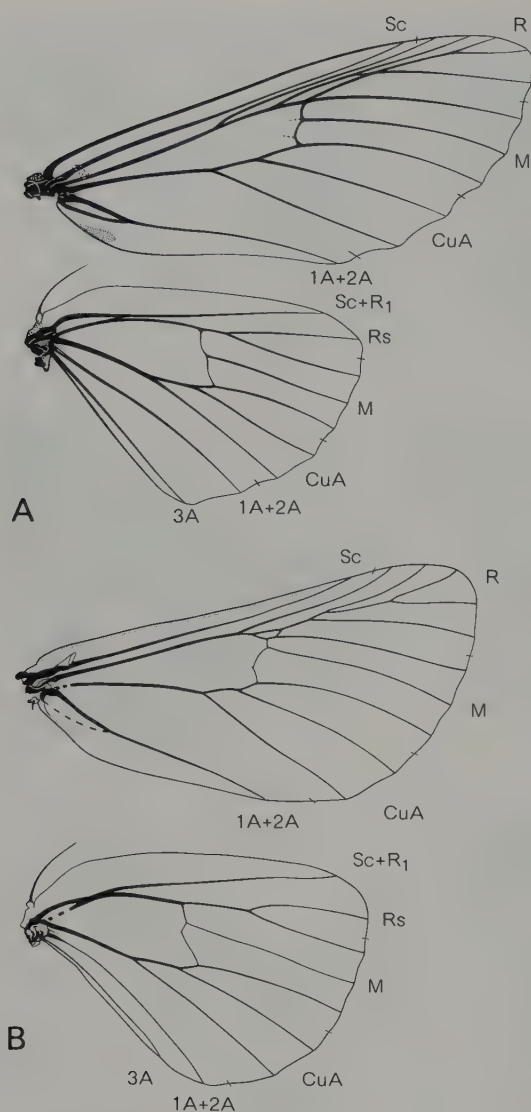


Fig. 41.73 Wing venation of Noctuoidea: A, *Sorama*, Notodontidae; B, *Ochrogaster*, Thaumetopoeidae.

[A by J. Wedgbrow; B by I. F. B. Common]

and often defoliate the tree; the larval hairs can cause irritating skin rashes. Less noticeable, processionary behaviour is displayed by *Epicoma* (18 spp.) and *Trichiocercus* (2 spp.). *E. melanosticta* (Fig. 41.72A) occurs widely in the east and south, the food plant being *Leptospermum*. In the white male of *T. sparshalli* the tegulae and tip of the abdomen both bear very long hair-scales. [Kiriakoff 1970]

**78. Lymantriidae** (tussock moths) (Figs 41.72C–E). Small to large; ocelli absent; antennae bipectinate to tip in male and usually in female, usually with 1–3 long terminal setae on each antennal branch; proboscis usually absent; maxillary palps 1-segmented or absent; epiphysis present in male, reduced or absent in female, tibial spurs short, 0–2–4, rarely 0–2–2; females sometimes brachypterous, flightless; fore wing (Fig. 41.74A) often with areole,  $R_3$  and  $R_4$  stalked from discal cell or areole,  $1A+2A$  simple; hind wing with Sc diverging from Rs at base but

approximated to, and usually connected with, Rs by  $R_1$  towards middle of discal cell (Fig. 41.76A), rarely fusing with Rs for short distance, Rs and  $M_1$  usually stalked,  $M_2$  arising nearer to  $M_3$  than to  $M_1$ ; thorax and abdomen densely hairy; abdomen with counter-tympanal hood prespiracular, abdominal segment 4 usually with pair of pockets, in female with dense anal tuft. Egg often hemispherical, rounded or subcylindrical, laid in cluster, usually covered with hair-scales from anal tuft. Larva with dense tufted secondary setae, often with 4 long dense dorsal tufts or with hair-pencils, a coloured dorsal gland on abdominal segment 6 and usually also on 7; external feeders, often arboreal. Pupa (Fig. 41.77D) stout, hairy, in silken cocoon incorporating larval hairs.

The family (Turner 1921) is best developed in the tropics, and has few endemic genera. Most species can be distinguished by the absence of the proboscis, by the position of  $M_2$  and of Sc in the hind wing, and by the prespiracular counter-tympanal hood. Adults sometimes rest with wings flattened against the substrate forming a triangle and the fore legs extended forward. In *Iropoca* (1 sp.), *Orgyia* (2 spp.) and *Teia* (2 spp.) there is an areole in the fore wing and females have abbreviated, crumpled wings; *Orgyia* and *Teia* lack medial spurs on the hind tibiae. *I. rotundata* (Fig. 41.72C) feeds on *Eucalyptus*, and the cocoons are spun beneath loose bark. *T. anartoides* from the south-east and *T. athlophora* (Fig. 41.72D) from the south-west are polyphagous pests of garden plants. The principal, native food plant of the former is *Acacia*. Most other genera lack an areole. The larvae of *Leptoncneria* (2 spp.) are urticating; *L. reducta* defoliates white cedar (*Melia*) in Qld and N.S.W. *Euproctis edwardsii* (Fig. 41.72E) also causes urticaria, and feeds on mistletoes, sheltering in crevices and beneath loose bark. To *Euproctis* (21 spp.), which is widely distributed abroad, belong smaller species, such as the orange *E. lucifuga* from Qld. It also includes small white or yellow species, such as *E. paradoxa* from eastern Australia. The endemic *Icta* (2 spp.) has narrow, elongate fore wings and short hind wings in the male, and short, functionless wings in the female. The larvae of *I. fulviceps* from N.S.W. feed on *Eucalyptus* foliage and shelter beneath loose bark. Adults of *Dura* (2 spp.) and *Lymantria* (4 spp.) are among the largest Australian lymantriids. [Ferguson 1978]

**79. Arctiidae** (Plates 7, G; 8, J; Figs 41.72F–I). Small to medium sized; head with short, lamellar scales; ocelli present or absent; antennae usually bipectinate or ciliate in male, simple in female; proboscis small or absent; maxillary palps tiny, 1-segmented; labial palps short, rarely long; epiphysis present, spurs 0–2–4 or 0–2–2; fore wing (Figs 41.74B, C) often without areole, Sc usually separate,  $R_2$  to  $R_5$  stalked,  $M_2$  arises much nearer to  $M_3$  than to  $M_1$ , or absent,  $1A+2A$  simple or with small fork; hind wing with Sc+ $R_1$  sometimes swollen at base, usually fused with Rs to near middle of discal cell, then divergent (Figs 41.76C–E),  $M_2$  arising nearer to  $M_3$  than to  $M_1$ ; often with dorsal prothoracic defensive glands; tympanal organs with tympanic membranes directed obliquely backwards; metathorax often with lateral tymbal organ; abdomen with counter-tympanal hood, if present, pre-



spiracular; ovipositor lobes with pair of glands, some females with terminal tuft of deciduous, long scales. Egg upright, usually hemispherical with raised network on surface, usually laid in cluster. Larva usually with dense secondary setae, in tufts, from verrucae, meso- and metathorax with 1 or 2 verrucae above spiracle; crochets uniordinal, abruptly shorter at end of each mesoseries; external feeders on herbaceous plants, or on lichens or dead leaves. Pupa (Fig. 41.77E) glabrous, cremaster weak or absent; in flimsy cocoon of felted larval hairs with little silk.

This family of often aposematically coloured moths is the second largest in the Noctuoidea; it has about 80 genera in Australia. The monophyly of the arctiids is perhaps best supported by the presence of a thoracic tymbal organ which is lacking in some wasp-mimicking ctenuchines (Kitching 1984b); the organ produces ultrasonic clicks that are thought to disrupt bat echolocation. The prothoracic gland is another apomorphy which, however, is not found in all species; it occurs widely in the Arctiinae and Lithosiinae. Many species are distasteful. Most species are nocturnal, but some are diurnal or dawn-flyers. Of the 4 recognised subfamilies the New World Pericopinae (Watson and Goodger 1986) are absent from Australia. [J. D. Holloway 1988]

ARCTIINAE (including Nyctemerinae; tiger moths) are robust, of moderate size, with fairly broad wings, frequently with black wing-maculation, striking wing patterns and red- or yellow-banded abdomen; ocelli present, proboscis reduced;  $Sc+R_1$  in hind wing swollen basally (Figs 41.74B, 76D); larvae densely hairy (woolly bears). *Nyctemera* (4 spp.) is widely distributed in the Oriental region and southern Pacific; the adults are day flying, migratory and come to light; the larva of *N. amica* (Fig. 41.72F) feeds openly on *Senecio*. *Argina astrea* has a boldly coloured, black and white larva that feeds on *Crotalaria*; the adult is rich orange with black spots. The cosmopolitan *Utetheisa* (3 spp.) includes *U. lotrix* (feeding on *Crotalaria*), *U. pulchelloides* (which occurs throughout Australia, feeding on Boraginaceae) and *U. pectinata* (from the northern N.T., where the larvae feed on *Argusia argentea*). Adults of *Rhodogastria* (5 spp.) produce quantities of frothy, orange fluid from their prothoracic glands and a sizzling sound when disturbed. *Spilosoma* (6 spp.) and *Amsacta* (5 spp.) have densely hairy larvae which usually feed on herbaceous plants; *S. canescens* (Fig. 41.72G) also attacks woody plants; *S. glatignyi* adults are very variable in the pattern on wings and abdomen. Females of *Phaos* (3 spp.) have atrophied wings and legs; the genus occurs in Tas. and in south-

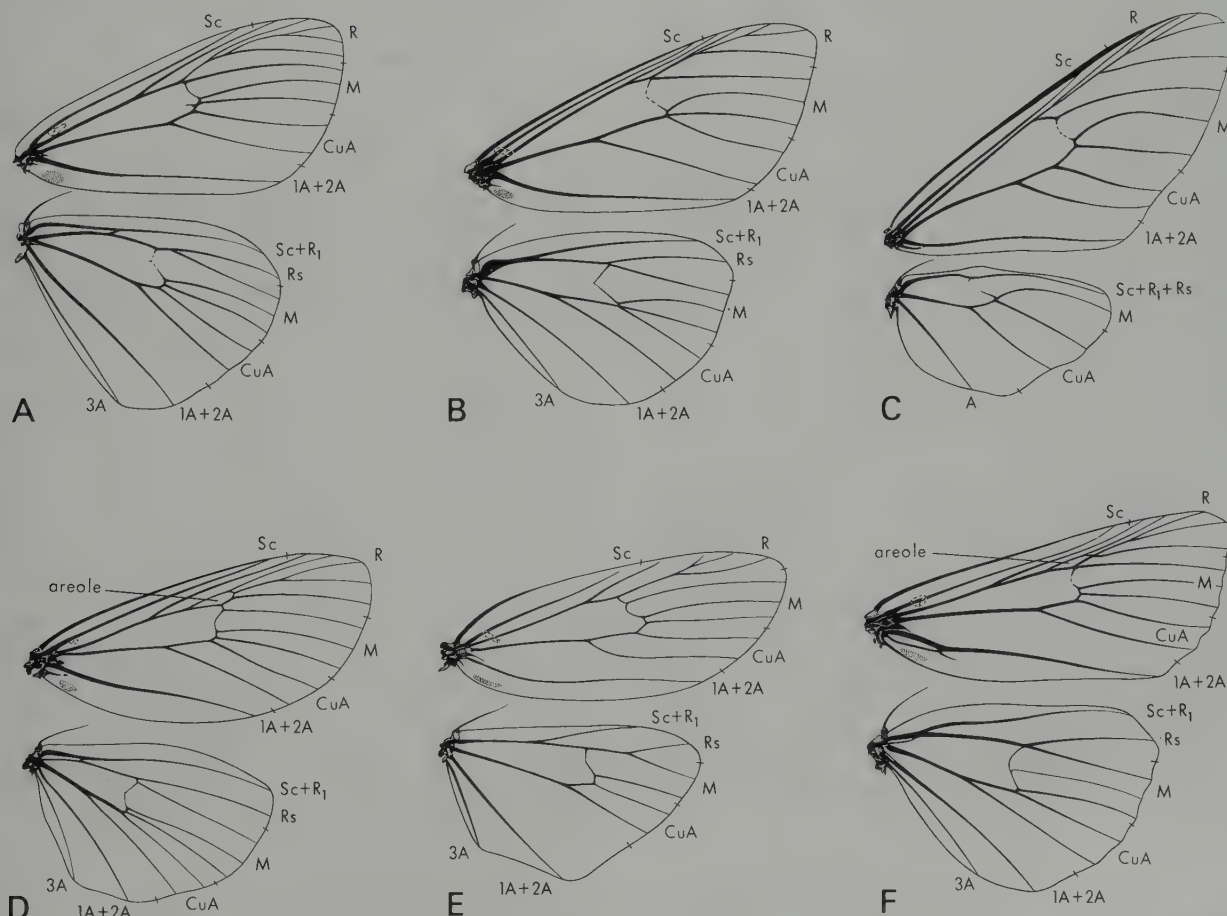


Fig. 41.74 Wing venation of Noctuoidea: A, *Leptocneria*, Lymantriidae; B, *Spilosoma*, C, *Amata*, Arctiidae; D, *Asota*, Aganaiidae; E, *Nola*, F, *Persectania*, Noctuidae. [J. Wedgbrow]

eastern mainland Australia at altitudes above 1500 m.

LITHOSIINAE are usually smaller and slender bodied, have narrow, almost rectangular fore wings and oval to rounded hind wings nearly equal in size to the fore wings; orange, red and black aposematic coloration is frequent but cryptic patterns occur; abdomen without segmental pattern; ocelli absent (in Australian species), proboscis often well developed; fore wing often with one vein lost ( $R_5$  or  $M_2$ ); larva usually less densely haired than arctiine larvae, on lichens, algae or moss. The subfamily is little studied. *Scoliacma bicolora* is a variable red and black species from the south-east, whereas the much larger *Oeonistis entella* (Plate 7, G) occurs in rainforest in northern Qld and New Guinea. *Halone coryphaea* is usually found resting on lichen-covered rocks, the cryptic fore wings covering the orange hind wings. *Thallarcha* (30 spp.) includes delicately patterned forms, such as *T. jocularis* (Fig. 41.72H) from the south-east. In *Xanthodula* (2 spp.) the female has rudimentary wings. *X. semiochrea* is thought to feed on lichens growing on trees and shrubs. *Termessa* (12 spp.) contains orange and black species, but also the delicate white *T. nivosa* with larvae found beneath loose bark on *Eucalyptus*.

CTENUCHINAE (Amatinae, Syntominiinae, Euchromiinae) have narrow, long fore wings and small, rounded hind wings, often white-tipped antennae, wings black with conspicuous orange dots or translucent spots, abdomen banded or brilliantly coloured; ocelli absent or present; without wing-locking microtrichia on fore wing; hind wing with  $Sc+R_1$  completely fused with  $R_s$  (Fig. 41.74C); tympanal and tymbal organs sometimes reduced or absent; larvae densely setose, meso- and metathorax with only 1 verruca above spiracle. A tropical subfamily, the Ctenuchinae are represented in Australia by *Euchromia* (4 spp.), *Eressa* (7 spp.), *Amata* (36 spp.) and *Ceryx* (4 spp.). They are diurnal and, with narrow fore wings, small hind wings, and ringed abdomen, rather resemble wasps. *Euchromia creusa* (Plate 8, J) is a brilliant species from northern Qld. *Amata* contains confusing black and orange species, in which the male retinaculum, ocelli and tympanal organs have been lost. The larvae are dark reddish black. Some, such as *A. aperta*, feed on living foliage, whereas others, such as *A. trigonophora* (Fig. 41.72I), feed on fallen flowers and leaves.

**80. Aganaidae** (Hypsidae) (Plate 8, H; Fig. 41.75A). Medium sized; ocelli present; antenna simple, ciliate in male; proboscis present; maxillary palps 1-segmented; labial palps ascending, apical segment long, slender, erect, smooth; epiphysis present; spurs 0-2-4; fore wing (Fig. 41.74D), with pouches in some males, sometimes without retinaculum,  $R_3$  and  $R_4$  stalked from areole,  $1A+2A$  with small fork or without fork; hind wing with  $Sc$  separate from  $R$ , with  $R_1$  joining it before middle of cell (Fig. 41.76B) or  $Sc$  separate from  $R$  at base but fused briefly with it before middle of cell,  $M_2$  arising nearer to  $M_3$  than to  $M_1$ ; thorax without tymbal; abdomen with prespiracular counter-tympanal hood. Larva noctuid-like, without ventral eversible organ on prothorax, only with primary setae, with only 1 subventral seta each on meso- and metathorax; on foliage. Pupa (Fig. 41.77F) with nar-

row strip of labial palp exposed, with curved groove in dorsal posterior margin of mesothorax and punctate abdomen, without cremaster, with terminal hooked setae; in cocoon or silk-webbing.

This small family of often aposematically coloured, arctiid-like moths has previously been associated with both the Arctiidae and the Noctuidae (Kitching 1984b). The adults of most Australian species are nocturnal and come to light.

Four genera are represented in Australia: *Digama* (1 sp.), *Agape* (1 sp.), *Asota* (5 spp.) and *Neochera* (1 sp.). The small *D. marmorea* is common and widely distributed in the north, with larvae on *Carissa ovata* (Apocynaceae). The larger *Agape chloropyga* (Plate 8, H) lacks a retinaculum in the male; its larva feeds on *Ficus*. The larvae of *Asota* also feed on *Ficus*; when young several rest together beneath a leaf, but later they are found singly. The dark brown larvae of *A. iodamia* (Fig. 41.75A) have short, white setae, and are found on *F. macrophylla*. [J. D. Holloway 1988]

**81. Herminiidae** (Figs 41.75B, C). Small to medium sized; ocelli present; antenna slightly shorter than fore wing, filiform or pectinate, male often with swelling before middle of flagellum; proboscis well developed; maxillary palps 1-segmented; labial palps long, usually sickle-shaped and upturned extending over head, rarely blade-shaped and porrect; epiphysis present; spurs 0-2-4; legs usually long and slender, male fore legs often modified and with hair-pencils; fore wing broad, often with costal fold in male, usually with areole,  $R_1$  arising beyond middle of cell,  $M_2$ ,  $M_3$  and  $CuA_1$  rarely stalked; hind wing with  $R_s$  and  $M_1$  fused or stalked,  $M_2$  well developed, rising above or at anal angle of cell; metathorax strongly swollen below tympanal organ; abdomen slender, first spiracle at lower margin or anterior margin of hood (prespiracular hood). Larva with 4 pairs of well developed ventral prolegs, granular cuticle, setae blunt, on small tubercles; usually on dead and decaying leaves. Pupa with cremaster, often with hooked spines; sometimes in slight cocoon among dead leaves.

A small and little-studied family in Australia best represented in the east and north. *Progonia patronalis* (Fig. 41.75C), from rainforest in southern Qld, is a small species with huge recurved labial palps. *Hydrillodes funeralis* has ciliate male antennae, upturned and apically expanded labial palps with specialised scales on the expanded portion, and the fore legs with large, concealed hair-pencils. *Simplicia circumscripta* (Fig. 41.75B), from eastern Qld, has a stout body, male antennae with a scaled knob at one-third, and the labial palps curved over the head; the legs of the male have a dense vestiture of hair-scales. [Owada 1987]

**82. Noctuidae** (Plate 8, M; Figs 41.75D-L). Small to large; ocelli usually present; antennae pectinate, dentate or simple; proboscis usually strong; maxillary palps 1-segmented; labial palps porrect or ascending; epiphysis present, tibial spurs 0-2-4, tibiae and tarsi sometimes spined; fore wing (Figs 41.74E, F) usually with areole,  $1A+2A$  forming basal fork; hind wing with  $Sc+R_1$  shortly fused with  $R_s$  near base (Fig. 41.76F), rarely fused to



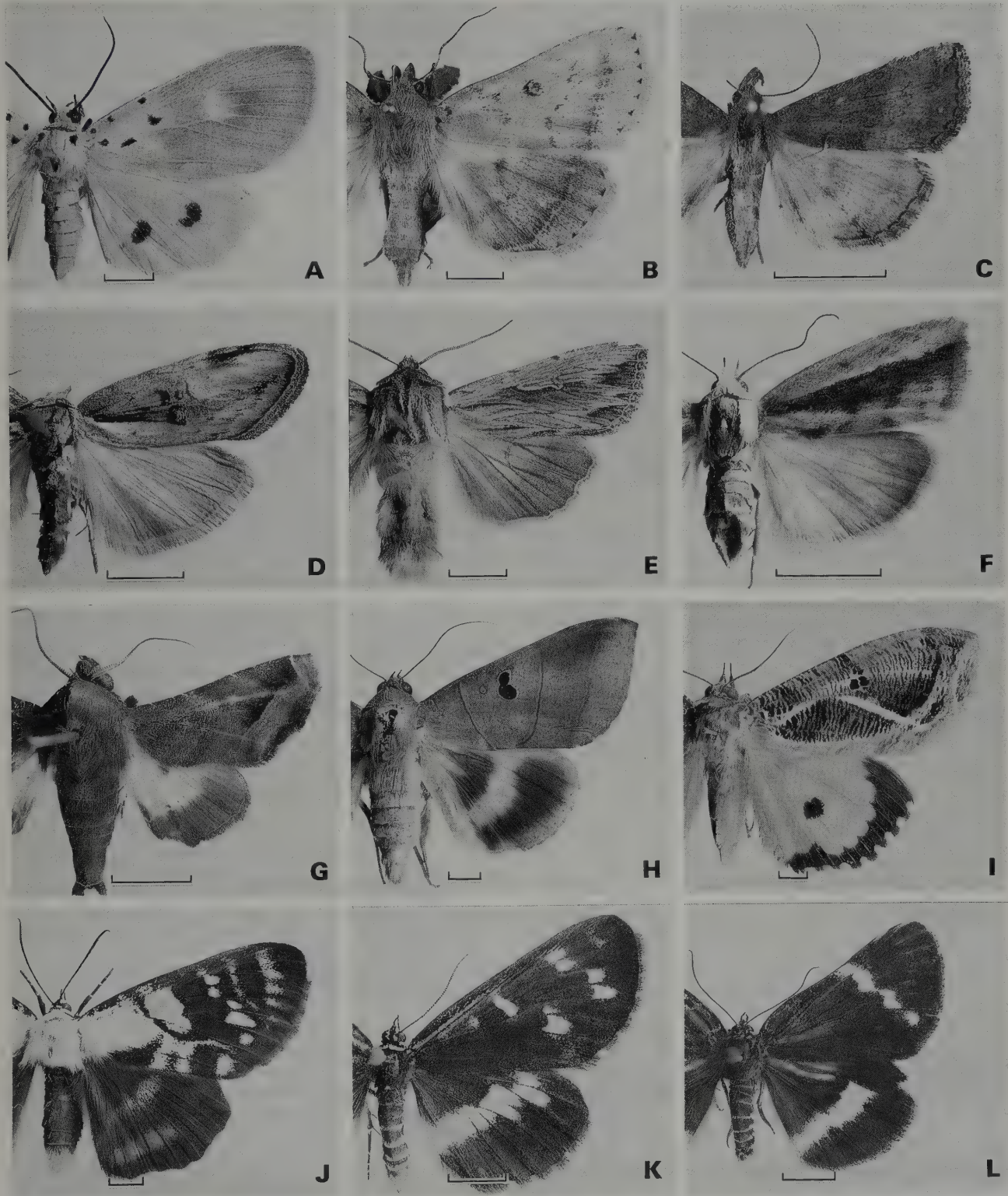


Fig. 41.75 A, *Asota iodamia*, Aganaidae; B, *Simplicia circumscripta*, C, *Progonia patronalis*, Herminiidae; D, *Aquita tactalis*, E, *Persectania ewingii*, F, *Earias perhuegeli*, G, *Penicillaria jocosatrix*, H, *Ophiusa coronata*, I, *Othreis materna*, J, *Agarista agricola*, K, *Cruria donowani*, L, *Platagarista macleayi*, Noctuidae. Scales = 5 mm.  
[J. Green, C. Lourandos]

about one-half of cell (Figs 41.76G),  $M_2$  weak and arising nearer to  $M_1$  than to  $M_3$  (trifid), or strong and arising nearer to  $M_3$  than to  $M_1$  (quadrifid); abdomen with counter-tympanal hood postspiracular. Egg usually domed, with vertical ribs, laid singly or in clusters. Larva usually without secondary setae, rarely with dense secondary setae on verrucae, crochets uniordinal, rarely biordinal, not abruptly shorter at ends of mesoserries; mostly phytophagous, sometimes stem boring, or predacious on coccoids (HEMI). Pupa (Figs 41.77G, H, J) in cell in soil, or in silken cocoon not incorporating larval hairs.

The family is one of the largest among the Lepidoptera with about 25 000 known species, all of which possess a postspiracular hood (Kitching 1984b). The family is divided into 20 subfamilies of which the Pantheinae are not known from Australia. The subfamilies are frequently divided into two dubious groups, trifinae (Amphipyridae–Heliethinae) and quadrifinae (Rivulinae–Plusiinae), based on the obsolescence or presence respectively of  $M_2$  in the hind wing. Perhaps more informatively, the male valvae of the trifine noctuids and Stictopterinae plus Plusiinae, the 'higher noctuids', usually have a clavus (a process from the dorsal margin of the sacculus) and many trifine males have paired hair-pencils at the base of the abdomen.

RIVULINAE are an ill-defined group with unlashed eyes and short labial palps. A few species, including *Rivula ommatopsis* from Qld, occur in Australia.

HYPENODINAE are mainly small species structurally similar to the Hypeninae but lacking ocelli. Species of both *Trigonistis* (2 spp.) and *Schrankia* (6 spp.) have long, straight labial palps.

HYPENINAE are weakly defined but usually recognised by their lashed eyes, presence of ocelli, slender body and long labial palps; the larvae are without prolegs on seg-

ment 3. *Hypena* (16 spp.) is the largest Australian genus. The larva of *H. laceratalis* from northern Australia attacks the weed *Lantana*.

CATOCALINAE (including Ophiderinae) have a smooth head, upturned labial palps with well-developed apical segment; often with spined tibiae and hair-pencil on mid tibia; male genitalia with fused pleural sclerites; larvae are semi-loopers with prolegs of segments 3 or 3 and 4 absent or reduced, pupa often with white waxy bloom. This is the largest noctuid subfamily with 10 000 named species world-wide and 400 in Australia; most species have a relatively robust body and broad wings (Fig. 41.75H). Adults of *Calyptra*, *Eudocima* and *Othreis* (Fig. 41.75I) are fruit-piercing and cause damage to citrus and soft fruits in Qld and N.S.W. *Dasypodia* contains large species with eye-spots; adults often enter houses and larvae feed mainly on *Acacia*. *Phyllodes imperialis* is a large rainforest species; the adults are attracted to fermenting fruit, as many other catocalines, and the cryptic, large larvae which display eye-spots and teeth-like marks when disturbed, feed on *Pycnarrhena*.

ACONTIINAE probably are polyphyletic and contain both trifid and quadrifid species. The larvae of some species of *Eublemma* (30 spp.) are predators on scale insects while larvae of *E. dimidialis* damage pods of mung beans. Larvae of *Enispa plutonis* live in spider webs and feed on remains of the spider prey. Males of *Amyna natalis* have a semi-transparent area in the fore wing and the larvae feed on *Sida*.

EUTELIINAE have a reduced female frenulum, anal hair-pencils in the male and adults rest with the abdomen curled up between the partly spread wings; without cremaster and anal hooks. A small subfamily with 19 named species in Australia. *Penicillaria jocosatrix* (Fig. 41.75G) larvae damage shoots and young fruit of mango. *Pataeta*

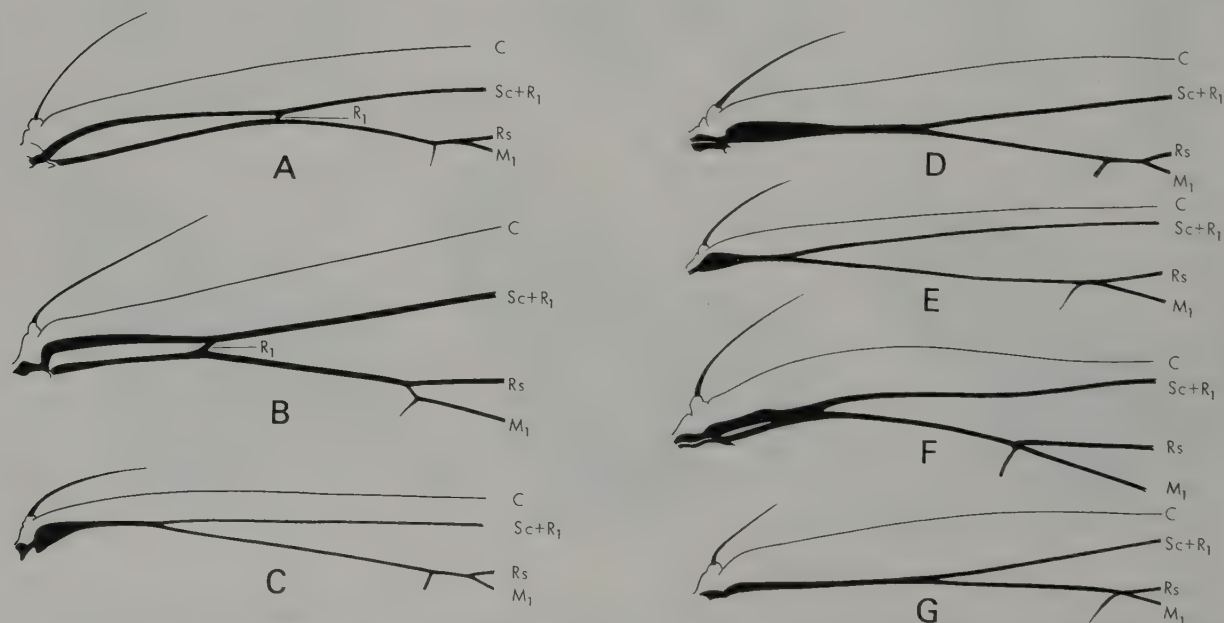


Fig. 41.76 Base of hind wing in Noctuoidea: A, *Euproctis*, Lymantriidae; B, *Asota*, Aganaiidae; C, *Nyctemera*, D, *Amsacta*, E, *Termessa*, Arctiidae; F, *Helicoverpa*, G, *Earias*, Noctuidae. [B. Rankin]



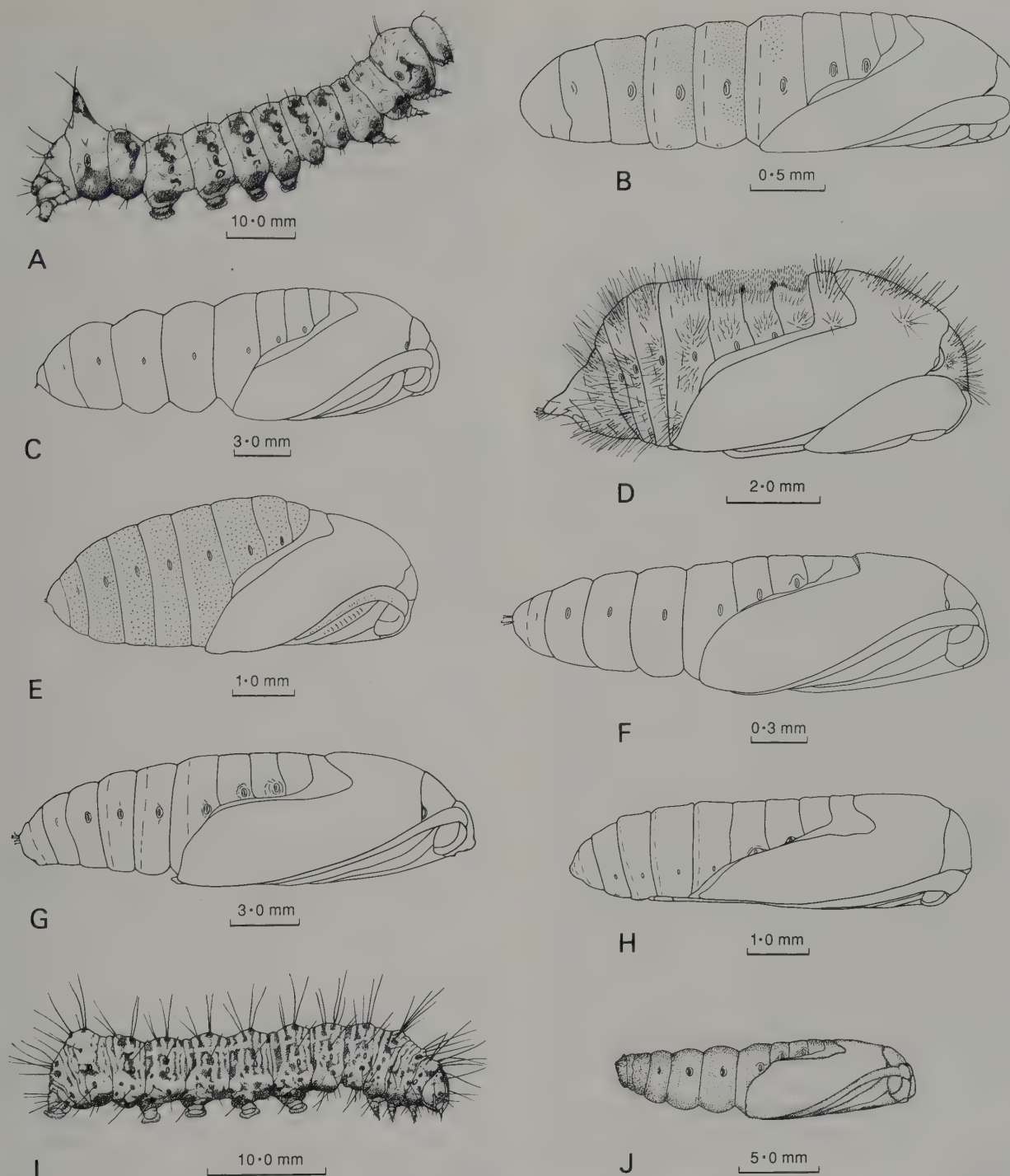


Fig. 41.77 Larvae and pupae of Noctuoidea: A, B, larva and pupa of *Danima*, Notodontidae; C, pupa of *Oenosandra*, Thaumetopoeidae; D, pupa of *Teia*, Lymantriidae; E, pupa of *Amsacta*, Arctiidae; F, pupa of *Agape*, Aganinae; G, H, pupa of *Cruria* and *Nola*, Noctuidae; I, J, larva and pupa of *Phalaenoides*, Noctuidae. [A, I, J by B. Rankin; B–H by I. F. B. Common]

*carbo* larvae feed on *Eucalyptus* and *Callistemon* (Myrtaceae) while other euteliine larvae feed mainly on Anacardiaceae.

NOLINAE are small, without ocelli, antenna bipectinate or ciliate in male, scape with tuft, fore wing with scales more or less raised and one or more scale-tufts (Fig. 41.75d); larva with dense secondary setae on verrucae,

segment 3 without prolegs; pupa without cremaster and hooked anal setae, in boat-shaped cocoon with vertical exit slit. *Uraba lugens*, with bipectinate male antennae, often defoliates *Eucalyptus*; the head capsules of the earlier instars are stacked upon the prothorax of the older larva. The largest genus in Australia is *Nola* (70 spp.).

CHLOEPHORINAE (Westermanniinae) have relatively

long upturned labial palps; smooth fore wing with bar-shaped retinaculum in male or retinaculum absent; larva with 4 pairs of ventral prolegs and only primary setae; pupa without cremaster, in boat-shaped cocoon with vertical exit slit. *Earias* (8 spp.) contains small, green and cream moths, with larvae in the seed capsules of Malvaceae; *E. perhuegeli* (Fig. 41.75F) and *E. vittella* are pests of cotton. *Aiteta iridias* is a medium sized, reddish brown rainforest species from Qld.

SARROTHRIPINAE, often small and grey, have long upturned labial palps; fore wings elongate with tuft of raised scales on cell, male retinaculum bar-shaped; larva with 4 pairs of ventral prolegs; pupa without cremaster, in boat-shaped cocoon with vertical exit slit. *Nanaguna breviscula* occurs through northern Australia and its larva feeds on *Grevillea*. *Calathusa* (17 spp.) is the largest Australian genus. A few species are placed in *Nycteola*.

STICTOPTERINAE have raised scale-tufts on fore wing, the basal half of the hind wing often hyaline, the female frenulum reduced, a double tympanal hood and a fork-shaped pupal cremaster. *Lophoptera vittigera* occurs widely in Asia, the south-western Pacific, Qld and eastern N.S.W. [J. D. Holloway 1985]

PLUSHINAE have a dorsal thoracic crest and dorsal abdominal tufts, lashed eyes, fore wing often with silver markings ('silver Ys'), metepimeron with distinct external bulge, double tympanal hood; larva without ventral prolegs on segments 3 and 4, crochets in biordinal mesoserries, without secondary setae; pupa in flimsy cocoon. *Chrysodeixis argentifera*, with both a silver Y and a silver S on the fore wing, is widely distributed in the South Pacific and is known to be a long-distance migrant; its larva is a pest of vegetables and ornamentals. *Thysanoplusia orichalcea* has established in eastern Australia; larvae feed on soybeans. Larvae of *Anadevidia peponis* feed on pumpkin and melon. [Kitching 1987]

AMPHIPYRINAE are a large ill-defined group; adults are stout, with eyes bare and unlashd, tibiae unspined; larvae often with terminal hump, without secondary setae. The striking *Cosmodes elegans* occurs widely in Australia; the larva feeds on *Lobelia* and *Verbena*. *Spodoptera* (7 spp.) is of economic importance; the adults are often migratory and larvae of *S. litura* feed on many crops while those of *S. exempta* may damage grasses. Larvae of *Bathytricha* bore in stems of grasses, including rice.

ACRONICTINAE are similar to Amphipyridae but the larvae have secondary setae. *Craniophora* is a possible Australian representative; its larva is unknown from Australia.

AGARISTINAE are usually brightly coloured, diurnal moths (Figs 41.75J-L); antennae usually thickened apically; tympanal hood small or absent, counter-tympanum large; larvae (Fig. 41.77i) aposematically coloured, with posterior hump; pupa well sclerotised, rugose, in cocoon. *Hecatesia* (3 spp.) contains the whistling moths; the males have a sound-producing device; a ribbed hyaline area lies adjacent to a large knob on the costa of each fore wing, and in flight the two knobs can be struck against one another above the body, flexing the ribbed membrane of the wings; the rapid succession of clicking sounds thus

produced resembles whistling. *H. fenestrata* (Plate 8, M) is common in the east. *Agarista agricola* (Fig. 41.75i) larvae feed on Vitaceae including grapevine. The larvae of *Phalaenoides glycinae* are pests of grapevines. *Apina callisto* occurs in southern Australia; the adults fly during autumn and the larvae feed during winter and pupate in a vertical tunnel in the soil. [Kiriakoff 1977]

CUCULLIINAE have bare, lashed eyes and unspined tibiae; larvae often feed on flowers and seeds. The subfamily contains only a few Australian species. *Neogalea sunia* has been introduced for the biocontrol of *Lantana*.

HADENINAE have hairy, unlashd eyes and unspined tibiae; eggs oblong, smooth, often laid in large clusters in a gel, sometimes in crevices; larvae often on Poaceae; pupa usually without cremaster but with anal, hooked setae. *Dasygaster padockina*, *Persectania* (Fig. 41.75E; 2 spp.) and *Mythimna* (11 spp.) are among the main pests of grasses and cereals; *M. convecta* is the common armyworm. *Tiracola plagiata* larvae damage bananas and also feed on melon and pumpkin. [Common 1954b, 1965a]

NOCTUINAE have bare, unlashd eyes and spined tibiae; larva unhumped, often burrowing. *Agrotis* (9 spp.) larvae (cutworms) are pests of many vegetables and field crops. *A. infusa*, the bogong moth, occurs through southern Australia; the adults aestivate annually on certain mountain tops in south-eastern Australia (Common 1954b, 1958a).

STIRIINAE. A small, mainly New World subfamily; larvae with scale-like spinneret. This subfamily is regarded as the sister-group of the economically important Heliothinae. *Austrazenia tusa* occurs in northern and western Australia and has been reared from native *Gossypium*. [M. Matthews 1987]

HELIOTHINAE have spiny-skinned larvae that feed mainly on seeds, fruits, flowers and flower-buds; adults often with tibial spines, hind wing with weak M<sub>2</sub> arising well above lower angle of cell and simple male genitalia; pupation in cell in soil. This subfamily is widely distributed in the arid tropics and subtropics and contains some of the world's most damaging pests of standing crops. *Helicoverpa armigera* and *H. punctigera*, widely distributed and native respectively, are the two most serious heliothine pests in Australia attacking cotton, tobacco, tomato, maize, sunflower and many other crops; adults are migratory. *H. assulta* occurs in South-East Asia and northern Australia while *H. prepodis* is an endemic and rare species. The large genus *Heliothis* is represented by 2 species in Australia. *Heliocheilus* is the largest genus in Australia with many species in the arid centre and north. [Common 1985; M. Matthews 1987]

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# Hymenoptera

(Wasps, bees, ants, sawflies)

I. D. NAUMANN

*With contributions by C. van Achterberg, T. F. Houston,  
C. D. Michener and R. W. Taylor*

Endopterygote Neoptera with mandibulate mouth-parts; wings with characteristic reduced venation and coupled by hamuli; abdominal segment 1 without sternum and closely associated with metathorax; commonly with constriction between abdominal segments 1 and 2. Larva eruciform in most Symphyta; apodous, usually maggot-like in Apocrita. Pupa aedeicous, generally exarate.

The Hymenoptera include as many species world-wide as either the Diptera or the Lepidoptera, and are more biologically diverse than any other hexapod order. They are outstanding among hexapods in the morphological features listed above, in the nearly universal haploidy of males and in the specialised forms of the ovipositor valves. The latter sometimes form blades, either simple or saw-like, and sometimes a hypodermic needle for the injection of venom.

There are two sub-orders. The **Symphyta**, with their phytophagous, caterpillar-like larvae, represent the most ancient radiation of the order. The **Apocrita** are today the more diverse, specialised and abundant sub-order and have adapted to parasitic, predatory, melliferous, fungivorous or scavenging life styles; larvae of some are phytophagous in plant galls. Apocrita exploit nearly all hexapod orders as hosts or prey, and make full use of the nectar and pollen resources of the flowering plants. Communal behaviour has developed many times within the Hymenoptera and some social bees and ants represent pinnacles of arthropod evolution. A few Hymenoptera are pests but generally 'no other order contains so many [species] that are of benefit to mankind' (Riek 1970).

Richards (1977) and Gauld and Bolton (1988) provide general introductions to the order and there are several outstanding biological reviews (Clausen 1940; Malyshev

1968; Askew 1971; Evans and Eberhard 1973; Hermann 1979–82). Krombein *et al.* (1979) cite much of the important, non-Australian literature.

## Anatomy of Adults

**Head** (Figs 42.1C–E). Orthognathous or prognathous; often very mobile. Compound eyes usually large, sometimes strongly convergent dorsally; fine setae sometimes emerging from between facets. Ocelli sometimes reduced or absent, especially in forms with reduced wings. Labrum sometimes concealed by clypeus. Occipital foramen and cavity containing mouth-parts sometimes separated by bridge formed by posteromedial extension of hypostoma, gena, postgena or postocciput.

The antennae (Fig. 42.2) are variable and often sexually dimorphic. Scape with basal ball-joint (*radicle*). Pedicel small. Flagellum primitively with many segments and the number of segments variable within a species. There is a tendency towards reduction in the number of segments and fixation on a particular number of segments. Nine segments (7 flagellar) are common in Symphyta and a combination of 13 segments in males and 12 segments in females is almost universal in Sphecoidea, Apoidea and Vespoidea.

The flagellum is sometimes differentiated into one or more ring-like segments (*anelli*), a *funicle* and a swollen,



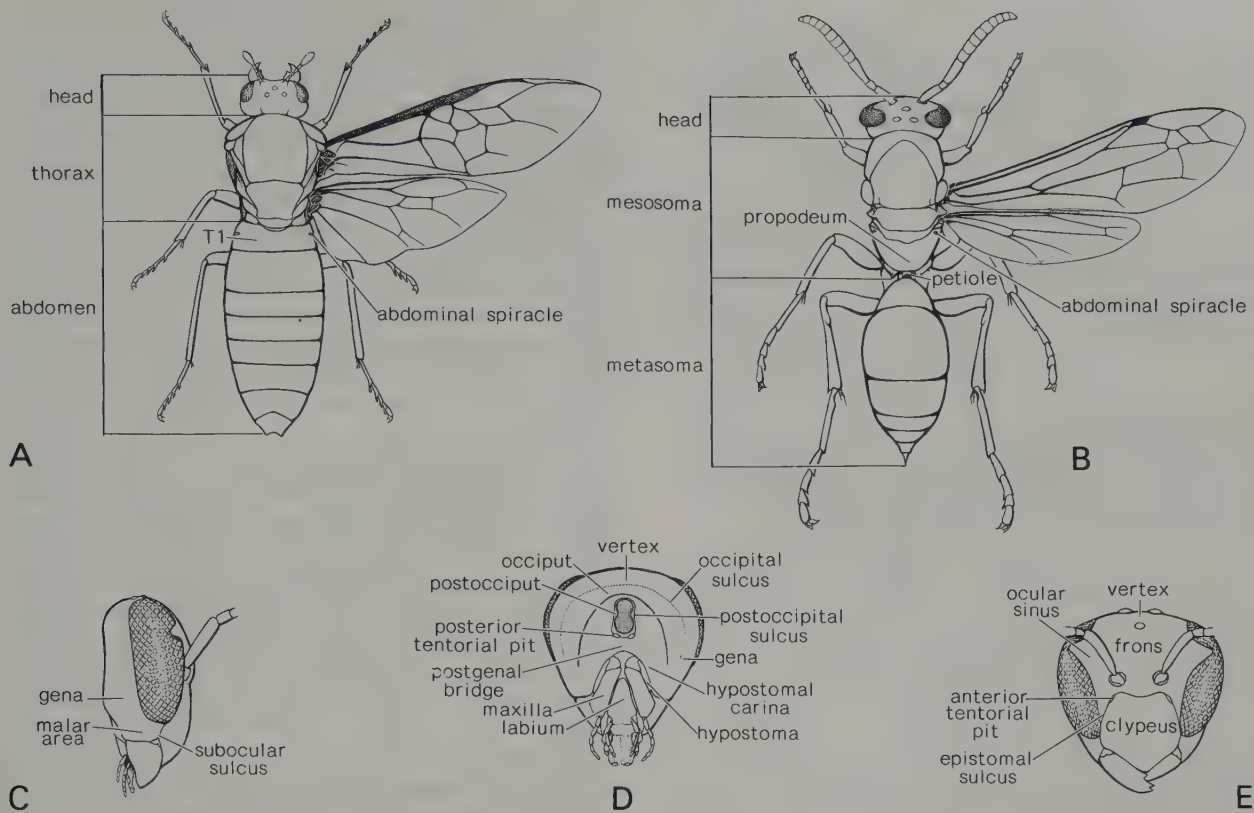


Fig. 42.1 Adults: A, Symphyta (*Perga* sp., Pergidae); B, Apocrita (*Polistes* sp., Vespidae). C–E, head of *Polistes*: C, lateral; D, posterior; E, frontal.

[S. Monteith]

distal *club*. In ants the pedicel plus the flagellum is called the funiculus. Commonly the antenna is more or less elbowed (*geniculate*) at the scape-pedicel joint.

The surfaces of the antennal segments, especially those of the flagellum, are covered with various sense organs, including some which are ridge-like (*multiporous plate sensilla*, tyloids, rhinaria).

At rest the antennae usually are directed anteriorly or dorsally, but if the flagellum is long it may be folded back over or under the body. In some Siricoidea, Stephanoidea and Megalyroidea the scape is folded ventrolaterally and rests in a *subantennal groove* below the eye (Fig. 42.3).

The mouth-parts (Fig. 42.4) vary from the generalised biting type of Symphyta and most Apocrita to the combined sucking and chewing type of advanced Apoidea. The mouth-parts are reduced in a few parasitic forms. Mandibles are usually present and used by the adult to cut its way out of the pupal cell (or host in the case of parasitic species), for defence, for killing and handling prey, and in nest construction. Maxillary palps 1–7-segmented, labial palps 1–4-segmented, palps sometimes absent. The labium and maxillae are sometimes elongate, forming a more or less retractile rostrum (proboscis) for nectar feeding. The glossae and paraglossae (*ligula*) are short in primitive Apoidea (cf. Fig. 42.43A) and elongate in the more highly evolved bees (Fig. 42.43B).

**Thorax/Mesosoma** (Figs 42.5, 6). Generally, in Hymenoptera abdominal segment 1 is associated closely with the metathorax. In Symphyta (Fig. 42.1A) the first,

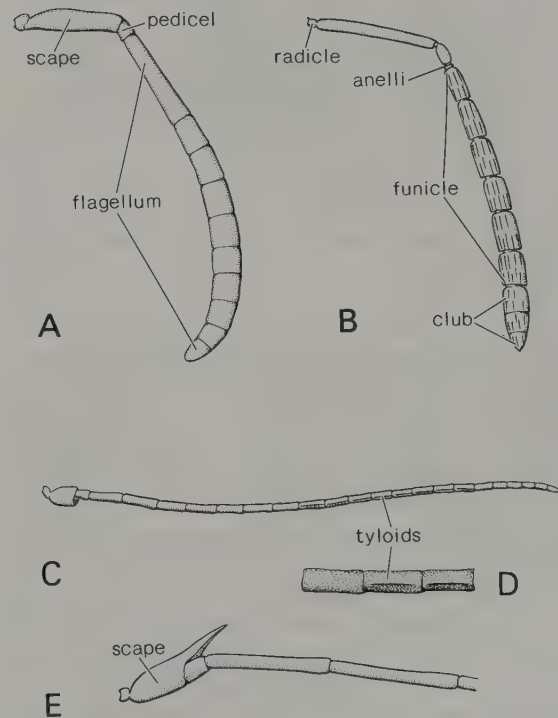


Fig. 42.2 Antennae: A, Vespidae; B, Chalcidoidea; C, D, Trigonalyidae; E, *Austroseserphus* sp., Proctotrupidae.

[S. Monteith]

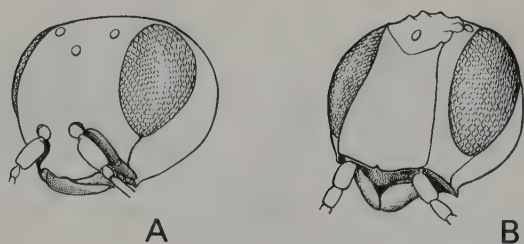
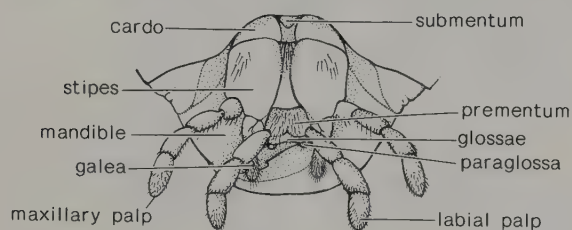
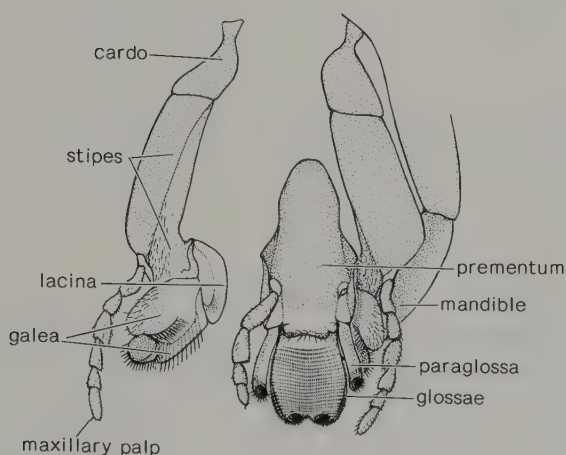


Fig. 42.3 Subantennal groove in: A, *Megalyra* sp., Megalyridae; B, *Guiglia* sp., Orussidae. [S. Monteith]



A



B

Fig. 42.4 Mouth-parts: A, *Perga* sp., Pergidae; B, *Polistes* sp., Vespidae. [S. Monteith]

post-cephalic tagma consists only of the 3 thoracic segments, but in Apocrita (Fig. 42.1B) abdominal segment 1 is attached firmly to the metathorax and usually is separated from the remaining abdominal segments by a narrow waist. This composite tagma of Apocrita (thoracic segments + abdominal segment 1) is termed the *mesosoma* or (mostly in ants) the *alitrunk*, and the incorporated abdominal segment 1 is the *propodeum* or (in ants) the *epinotum*.

Primitively the pronotum is dorsally large with a straight posterodorsal margin, is loosely attached to the mesothorax and propleura, and has rounded ventrolateral corners. In a common, more advanced condition (e.g. in Vespidae) there is a loss of mobility on the mesothorax, the posterodorsal margin is strongly emarginate, and the ventrolateral corners are acute. These forms with a less

mobile pronotum tend to be strong fliers. Sometimes the pronotum extends ventrally to the mid-line to form a complete ring. In the primitive condition (e.g. many Symphyta) the mesothoracic spiracle is exposed in the membrane between pronotum and mesepisternum. The pronotum is often posteriorly produced dorsal to, ventral to, or over the top of the spiracle. The *spiracle cover lobe* (pronotal tubercle) is margined with close, fine hairs in Trigonalidae and many aculeates. The propleura resemble basal segments of the legs and often meet along the mid-line, concealing the prosternum. Usually the pronotum is differentiated into an attenuated, anterior *neck* and an expanded, posterior *collar*. The membrane between the neck and head contains *cervical sclerites* in a few Symphyta.

The mesothorax is large to accommodate the major flight muscles which move the fore wings. The mesonotum is divided into an anterior scutum and a posterior scutellum, separated by the scutoscuteal suture. The mesoscutum often has longitudinal grooves, including: the *median line* (*median sulcus*); the paired *notauli*, which delimit a *median mesoscutal lobe* from the *lateral mesoscutal lobes*; and the *admedian lines*. Each lateral mesoscutal lobe sometimes has a longitudinal groove or ridge, the *parapsidal line* which delimits a lateral area, the *parapsis*. In some Symphyta and most Apocrita the posterodorsal portions of the mesoscutum are segregated by a transverse line of flexibility, the *transscutal articulation*, and are delimited as *axillae* beside the mesoscutellum. A mesopostnotum is present in some Symphyta.

The mesepimeron is large in Symphyta and some Chalcidoidea, but reduced in most Apocrita, sometimes to a narrow, sculptured strip behind the enlarged mesepisternum. The pleural sulcus is sometimes absent.

The mesopleural and mesosternal regions are not clearly differentiated. The mesothorax has a mid-ventral line (discrimen) and in most Hymenoptera the only recognisable mesosternal elements appear to be some small sclerites immediately anterior to the mid coxae. The mesopleuron has various, secondary grooves and carinae (e.g. *pre-episternal groove*, *sternaulus*) which are of considerable taxonomic importance.

A post-spiracular sclerite is present in most Symphyta between the anterodorsal mesepisternum and the pronotum; it is absent in Apocrita. Below the postspiracular sclerite is the *prepectus*, which is sometimes concealed beneath the pronotum, sometimes secondarily fused to the pronotum (and recognisable only as an internal ridge—the *posterior pronotal inflexion*) and sometimes fused to the mesepisternum. Fusion of the prepectus to the pronotum may result in the mesothoracic spiracle opening through the apparent pronotum (e.g. Megalyridae, Proctotrupidae, Ceraphronoidea).

The metathorax bears the hind wings and is smaller and less differentiated than the other thoracic segments. The metanotum of Symphyta (except in the extralimital Cephidae) bears roughened lobes (*cenchri*) and in Apocrita tends to be invaginated or fused to adjacent sclerites. In Sphecoidea and Apoidea the metapostnotum is greatly enlarged and forms the dorsal 'triangular area' of



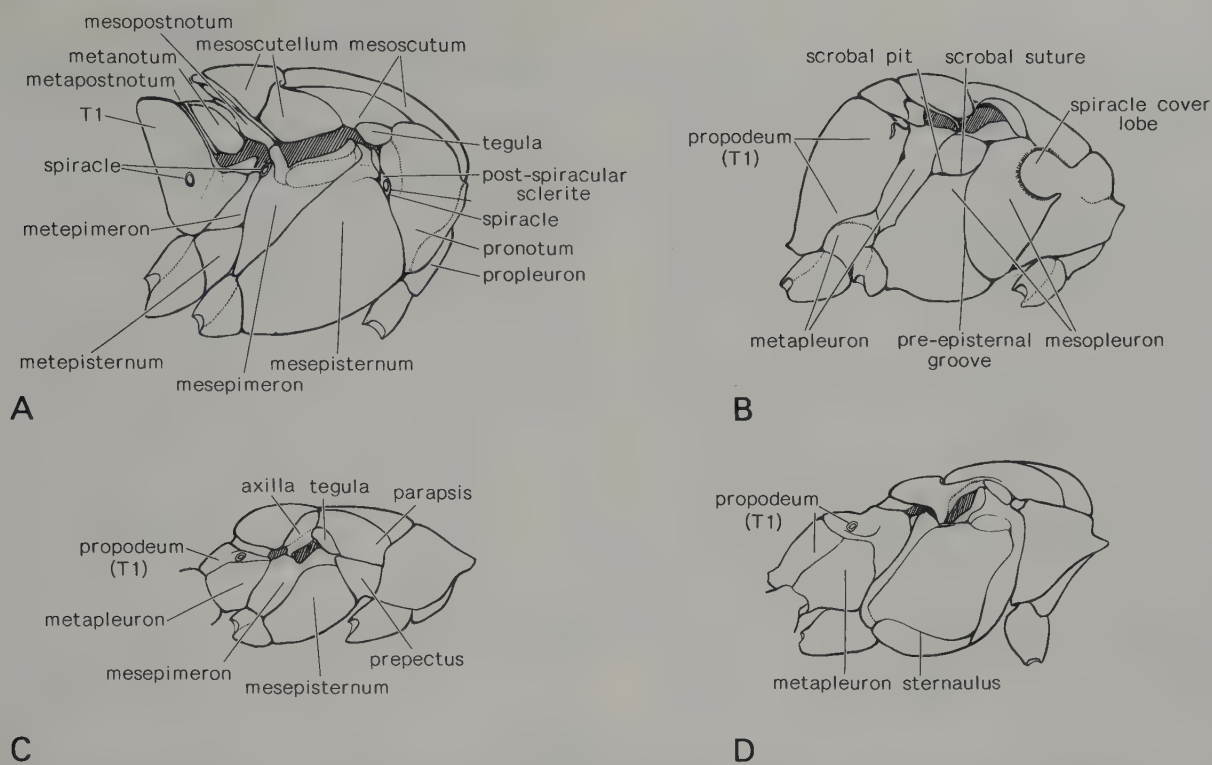


Fig. 42.5 Lateral thorax: A, *Perga* sp., Symphyta-Pergidae; B, *Hyleoides* sp., Apoidea-Colletidae; C, *Thaumasura* sp., Chalcidoidea-Pteromalidae; D, *Ceratomansa* sp., Ichneumonidae. [S. Monteith]

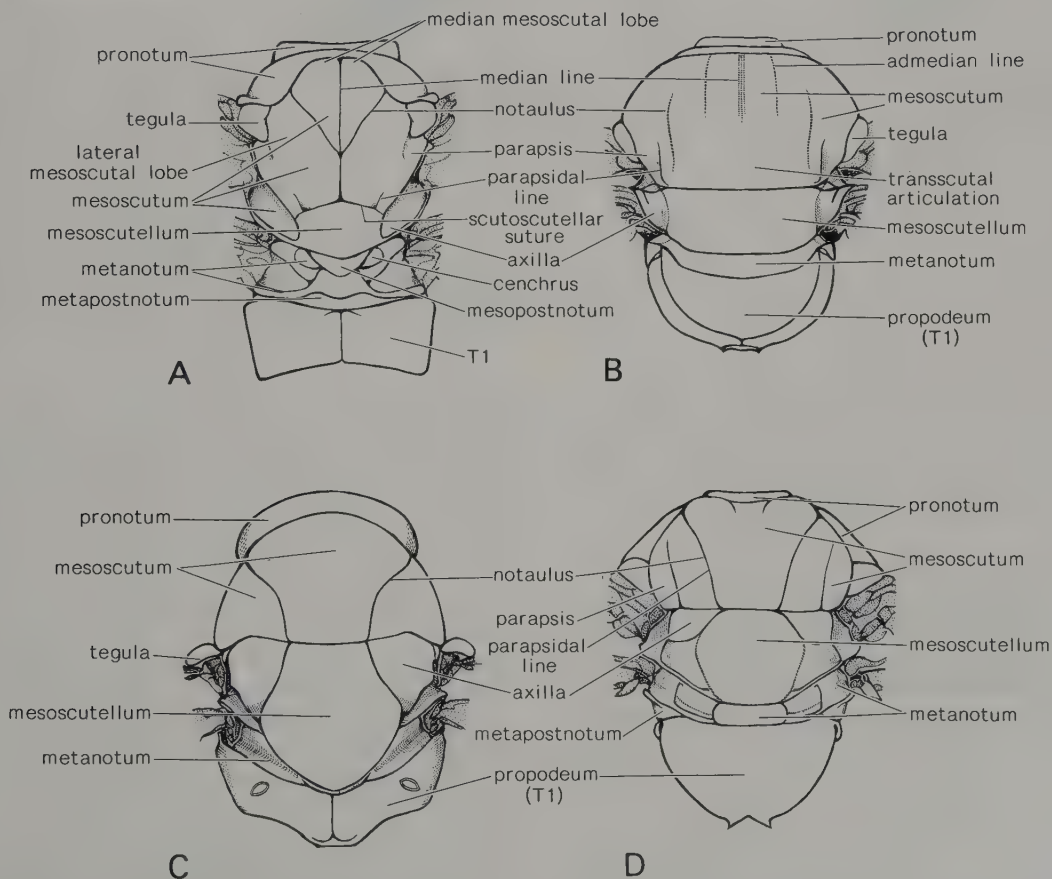


Fig. 42.6 Dorsal thorax and propodeum: A, Symphyta-Tenthredinidae; B, *Sphecius* sp., Sphecidae; C, *Agamerion* sp., Pteromalidae; D, *Taeniogonalos* sp., Trigonalidae. [S. Monteith]

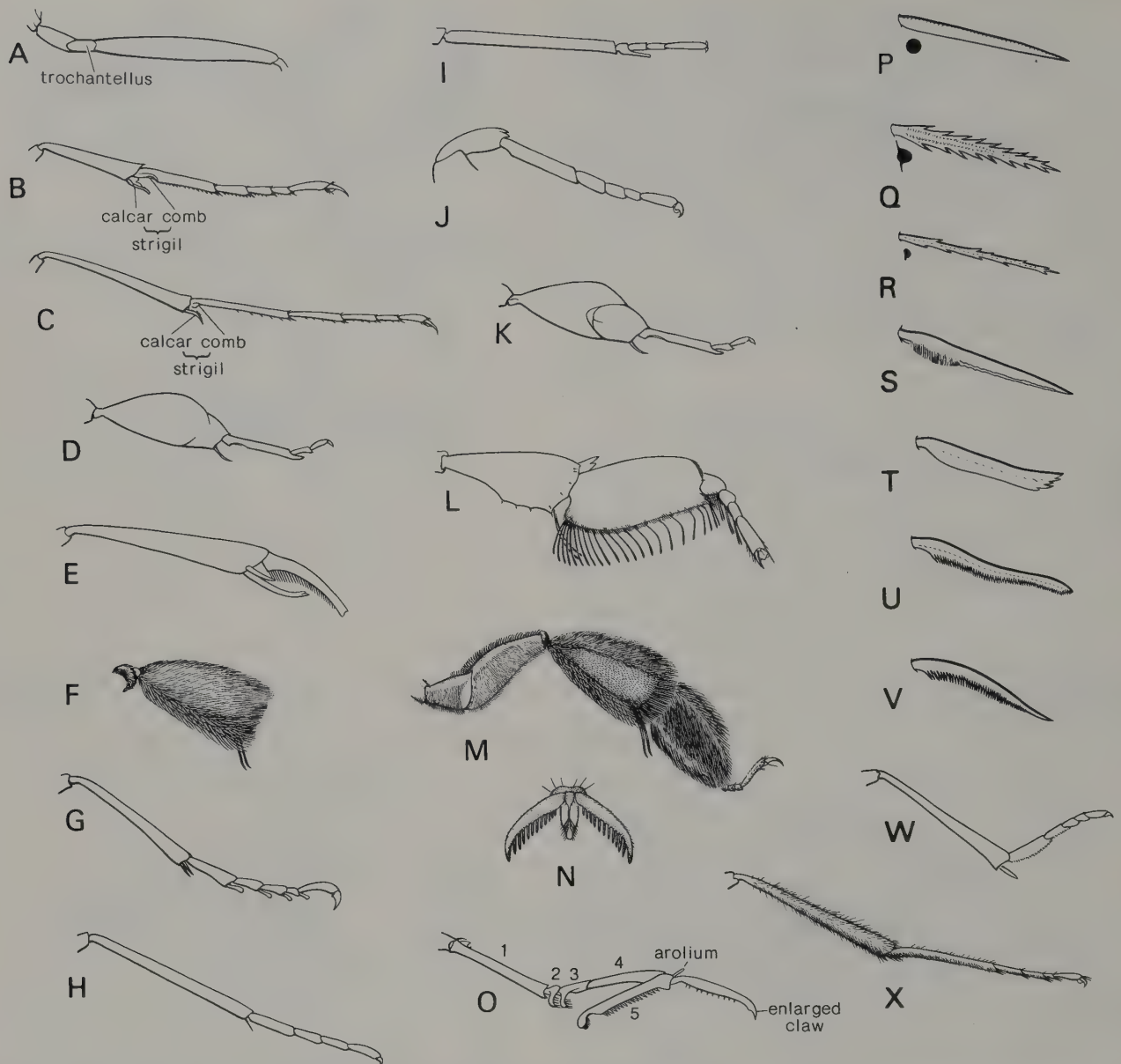


Fig. 42.7 Legs: A, hind, of *Ceratomansa* sp., Ichneumonidae; B, fore, C, hind, of *Sceliphron* sp., Sphecidae; D, fore, of *Guiglia* sp., Orussidae, ♀; E, fore, of Ceraphronidae; F, hind tibia, of *Amegilla* sp., Anthophoridae; G, fore, of *Perga* sp., Pergidae; H, fore, of *Elasmus* sp., Elasmidae; I, hind, of *Ibalia* sp., Ibalidae; J, fore, of *Pleistodontes* sp., Agaonidae; K, fore, of *Guiglia* sp., Orussidae, ♀; L, fore, of *Bembix* sp., Sphecidae; M, hind, of *Amegilla* sp., Anthophoridae; N, claws of *Netelia* sp., Ichneumonidae; O, fore, of *Dryinus* sp., Dryinidae, ♀; P–V, mid or hind tibial spurs (P, simple; Q, R, flattened, with dentate margins; S–V, modified to form calcar); W, mid, of Eupelmidae; X, hind, of *Megalyra* sp., Megalynidae.

[A–O, W, X by S. Monteith; P–V after Brothers 1975]

the propodeum. The metathoracic spiracle is sometimes visible close to the base of each hind wing. The metapleuron is either divided into distinct metepisternum and metepimeron, or represented by a simple plate; in some Apocrita the metapleuron is obscurely separated from the propodeum.

The propodeum, which is present only in Apocrita, has a conspicuous pair of spiracles.

In Hymenoptera with reduced wings (e.g. Fig. 42.32E) the mesosoma is often highly modified by enlargement of the pronotum, reduction of the mesonotum, loss of various grooves, and fusion of sclerites (Reid 1941).

**Legs** (Fig. 42.7). Occasionally the coxa has an annular constriction (*basicoxal groove*). A trochanter is present. The proximal end of the femur is sometimes separated from the rest of the femur by an annular groove. The separated portion (the *trochantellus*, Fig. 42.7A) is large and freely articulated in many Symphyta and terebrant Apocrita. An analogous *basal ring* is defined on the femur of some aculeates.

The tibiae have ventro-apical, articulated spurs (Figs 42.7P–V). Typically in Symphyta the fore, mid and hind legs each have 2 such spurs (i.e. *tibial spur formula* 2-2-2). In Apocrita the tibial spur formula commonly is 1-2-2



or 1-1-2. Tibial spurs may be variously modified, reduced or lost. Some Symphyta have 1-4 articulated, preapical tibial spurs (Figs 42.16B-D, F, G).

Primitively the tibial spurs are simple, straight and similar to each other. Where the fore tibial spurs are of this form, both fore legs are used together to clean each antenna. In more advanced Symphyta the anterior (inner) of the 2 fore tibial spurs is curved, sometimes expanded and margined with setae, and thus modified into a *calcar*. The first tarsal segment (*basitarsus*) may then have an adjacent comb of setae. The calcar and comb together comprise the *strigil* (Fig. 42.7B). Each antenna is cleaned by being dragged through the opening between calcar and comb on one fore leg (Schönitzer and Lawitzky 1987). The fore legs are also used to clean the face and eyes, and are in turn cleaned by the mouth-parts.

Most Apocrita have a well-developed strigil on the fore leg. Ceraphronoidea (Fig. 42.7E) and some male *Nothomyrmecia* (Formicidae) have 2 fore tibial spurs but all other Apocrita have one or none. The fore tibial spur is short and straight in Eulophidae and Elasmidae (Fig. 42.7H) and in at least some eulophids both fore legs are used together to clean each antenna.

The inner hind tibial spur forms a calcar in most Chrysidoidea, Sphecoidea, Apoidea, Pompilidae, Rhopalosomatidae, Vespidae and Formicidae (Fig. 42.7C). Hind tibial spurs are absent in a few bees and ants, and many bees and ants have calcar-like spurs on all legs. There is sometimes an inner preening brush of setae on the hind tibia and sometimes the basitarsus (Fig. 42.7X). The hind legs are used to clean the wings, metasoma and mid legs and the hind legs themselves are cleaned by being rubbed and scraped against each other.

Normally the tarsi are 5-segmented, but in some Chalcidoidea and Platygasteridae there are 4 segments, and in Trichogrammatidae only 3. Membranous, ventral pads (*plantar lobes*) are present on each tarsal segment of many Symphyta (Fig. 42.7G) and some Apocrita. The apical tarsal segment bears 2 claws, these being either simple or with ventral teeth (Fig. 42.7N). Usually there is a pad-like *arolium* between the claws.

The legs are sometimes highly modified. Fossorial species often have robust legs, stout tibial setae and broadened tarsal segments. A comb (*pecten*, Fig. 42.7L) of long tarsal setae is commonly present, especially on the fore leg of ground-nesting aculeates, and is used to rake soil particles. The outer, proximal part of the hind tibia forms a flattened *basitibial plate* in ground-nesting bees and Sphecidae, and probably assists the insect to move about in burrows.

In many Chalcidoidea the mid legs are modified for jumping: the tibial spur is enlarged and the tarsal segments are often enlarged with ventral rows or pads of stout setae (Fig. 42.7W).

The expanded fore tarsi of some male Megachilidae are important in courtship. The raptorial fore tarsi of most female Dryinidae (Fig. 42.7O) grip the host during oviposition. The hind femora (or very rarely the fore femora) are enlarged and toothed in some terebrant Apocrita (e.g. Figs 42.25B, C, E, G).

In most Apoidea modified grooming movements of the legs transfer pollen from various parts of the body to either the mouth-parts or the specialised, pollen-carrying areas of the body surface (Jander 1976). Commonly the hind tibia and basitarsus are enlarged, with long hairs on their outer surfaces (Figs 42.7F, M). These hairs form either a brush (*scopa*) or are reduced to a fringe surrounding a bare area or concavity (in which case the whole is termed a *corbicula* or *pollen basket*). Megachilidae have a well-developed scopa on the ventral surface of the metasoma.

**Wings** (Figs 42.8, 9). Two pairs of wings are usually present. The membranes are mostly hyaline and covered with fine microtrichia, and the wing margins of small species often have long fringes. A scale-like tegula covers the base of the fore wing.

Wing venation terminology is given in Figs 42.8A, C, E, H, 9A. In the fore wing Rs is fused with M for part of its length, M is unbranched and CuP is absent. The venation is most complete in Symphyta (e.g. Figs 42.8A, 16) and most reduced in small Apocrita (e.g. Figs 42.8E, 23, 25). The portion (intercept) of R1 between its junction with Rs and the pterostigma is termed the *parastigma* (prestigma). Figs 42.8B, D, 9B give cell nomenclature. Cell 3R1 is sometimes termed the *marginal cell*, and 1+2R1, 1Rs and 2Rs respectively the 1st, 2nd and 3rd *submarginal cells*. 1Rs is also known as the *areolet*.

Rows of hooks (*hamuli*, Figs 42.8F, G) on the leading edge of the hind wing engage the hind margin of the fore wing, and strongly couple the wings in flight. There are few hamuli (usually only 2 or 3; Fig. 42.8G) in small species, and many (Fig. 42.8F) in strong-flying, larger wasps and bees. The fore margin of the hind wing sometimes has additional, hooked or slightly curved microtrichia ('secondary hamuli'). The 'secondary hamuli' also assist in wing-coupling and may form a continuous row from wing base to hamuli, or may be clustered basally and near the hamuli. The fore wings remain coupled when at rest in some Hymenoptera.

The fore wings are longitudinally folded at rest in many Vespidae (Fig. 42.8I), all Gasteruptiidae and Leucospidae, and some Figitidae, Diapriidae, Pompilidae and Colletidae (Danforth and Michener 1988).

The wings are reduced or absent in a few extralimital Symphyta and in many Apocrita. All worker ants (Figs 42.34, 36, 40) and all female Mutillidae (Fig. 42.32B) and Thynninae-Tiphiidae (Figs 42.32E, F, H) are apterous. Brachypterous or apterous females occur in many Ceraphronoidea (Fig. 42.17E), Diapriidae, Platygasteroidea (Figs 42.23D, F, J), Chalcidoidea (Fig. 42.26G) and Chrysidoidea (Figs 42.23C, G, J), a few Ichneumonoidea (Fig. 42.20G), Megalynidae, Rhopalosomatidae (Fig. 42.30I) and Pompilidae, and in many (mostly extralimital) Cynipidae. Wing-reduced males are less common but include some bizarre forms (e.g. Fig. 42.26C) which develop in concealed niches and disperse little or not at all after emergence. Alary polymorphism occurs in some species. Extremely modified, apterous forms are sometimes difficult to identify to family.

**Abdomen/Metasoma** (Fig. 42.10). In Symphyta





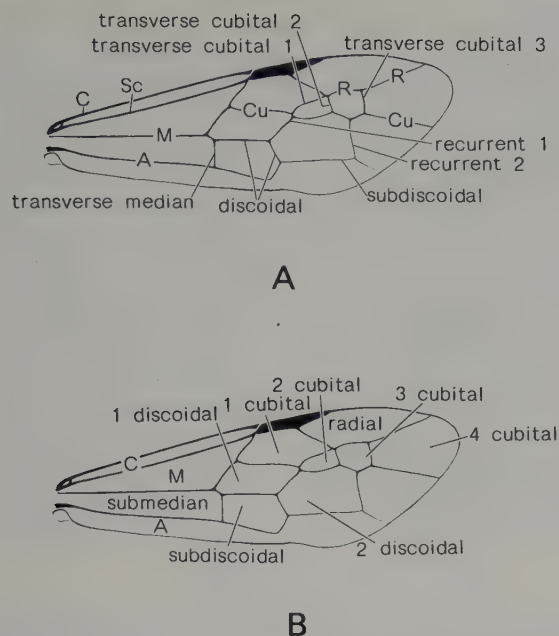


Fig. 42.9 Wing, other terminologies (*Taeniogonalos* sp., Trigonalyidae). [S. Monteith]

the remaining abdominal segments form the *metasoma* which is usually separated from the propodeum by a pronounced constriction or waist (Fig. 42.1B). In Apocrita in which the metasoma is broadly joined (sessile), a massive phragma projects from the mesosoma into the following segments.

The *petiole* is the narrow, constricted zone at the base of the metasoma. Usually the petiole is formed by all or only the anterior part of abdominal segment 2 (= metasomal segment 1). If only the anterior part of the abdominal segment 2 is narrowed, the swollen posterior part is sometimes termed the *postpetiole*. In Mymarommatidae (Fig. 42.25D), the extinct Serphitidae and some ants abdominal segments 2 and 3 form a 2-segmented petiole and in ants abdominal segment 3 is termed the postpetiole (Fig. 42.34). In this chapter, the *gaster* is regarded as that part of the metasoma posterior to the petiole (irrespective of the segmental composition of the petiole) but for some authors the terms *gaster* and *metasoma* are synonymous. In some Hymenoptera in which both the tergum and sternum of abdominal segment 2 (i.e. T2, S2) are anteriorly narrowed, one or the other is excluded from the actual articulation with the propodeum. In a few Hymenoptera the petiole is formed entirely by either the tergum or the sternum. The tergum and sternum of the petiole are often fused to form a cylinder or ring.

Eleven abdominal segments can be distinguished in some Symphyta although T11 is membranous and attached to T10. Generally in Hymenoptera fewer than 10 abdominal segments are visible externally. Either terga and sterna are fused to form *synterga* or *synsterna*, or posterior segments are desclerotised and/or telescoped within preceding segments. *Laterotergites* and *laterosternites* are sometimes defined laterally. Terga and sterna usually overlap to conceal the intervening membrane, but

sometimes tergum and sternum of a particular segment are fused to each other.

Functional spiracles are present on abdominal segments 1–8 in most Symphyta and some Apocrita (e.g. Ichneumonidae), but the metasomal spiracles are variously reduced in many Apocrita, e.g. present only on metasomal segment 7 in Proctotrupoidea, Chalcidoidea and Cynipoidea; absent entirely in Platygasteroidea.

A pair of *cerci* (pygostyles) is associated with the apical tergum. The cerci are finger-like and 1-segmented, or reduced to pads with sensory hairs (*trichobothria*). They have been lost entirely by female aculeates.

The terga sometimes bear specialised ridges or depressions. The lateral fovea between the base and the spiracle of T2 is termed the *glymma* (Ichneumonidae, Fig. 42.10E) or *dorsope* or *laterope* (van Achterberg 1976a; Braconidae), and depressions on both sides of T3 are *gastrocoeli*. In fossorial forms the apical tergum (*pygidium*) sometimes has a flattened area defined by carinae (the *pygidial plate* (Fig. 42.41B)); presumably this assists the wasp or bee in digging or moving about in the burrow.

The male terminalia (Fig. 42.11) consist of a *basal ring* (*gonobase*); a median intromittant organ (*aedeagus*) with associated *aedeagal apodemes*; a pair of *volsellae* closely associated with the aedeagus; and a pair of outermost structures, the *parameres* (Snodgrass 1941). The volsellae are small pincers which grasp the genital membranes of

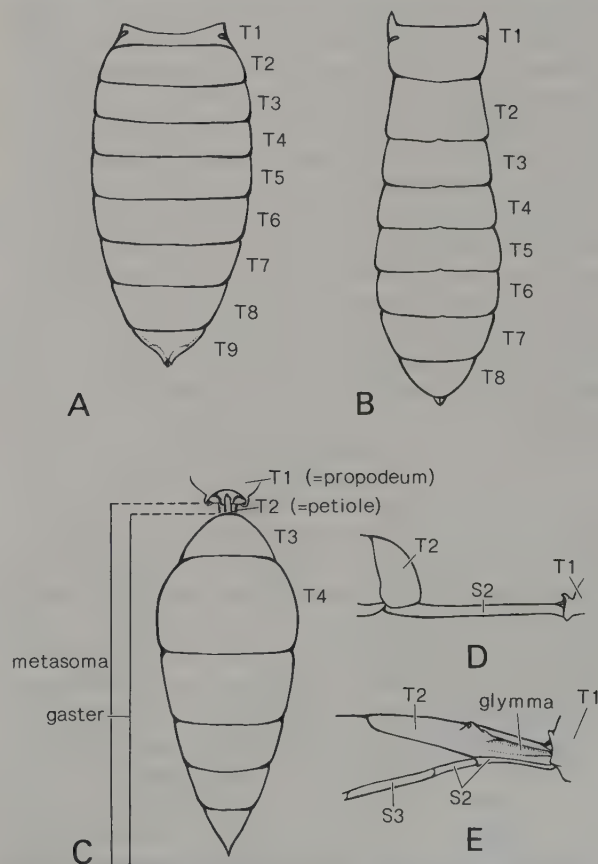


Fig. 42.10 Abdomen: A, *Perga* sp., Symphyta-Pergidae; B, *Guiglia* sp., Symphyta-Orussidae; C, *Polistes* sp., Apocrita-Vespidae; D, *Sceliphron* sp., Sphecidae, lateral; E, *Netelia* sp., Ichneumonidae, lateral. [S. Monteith]

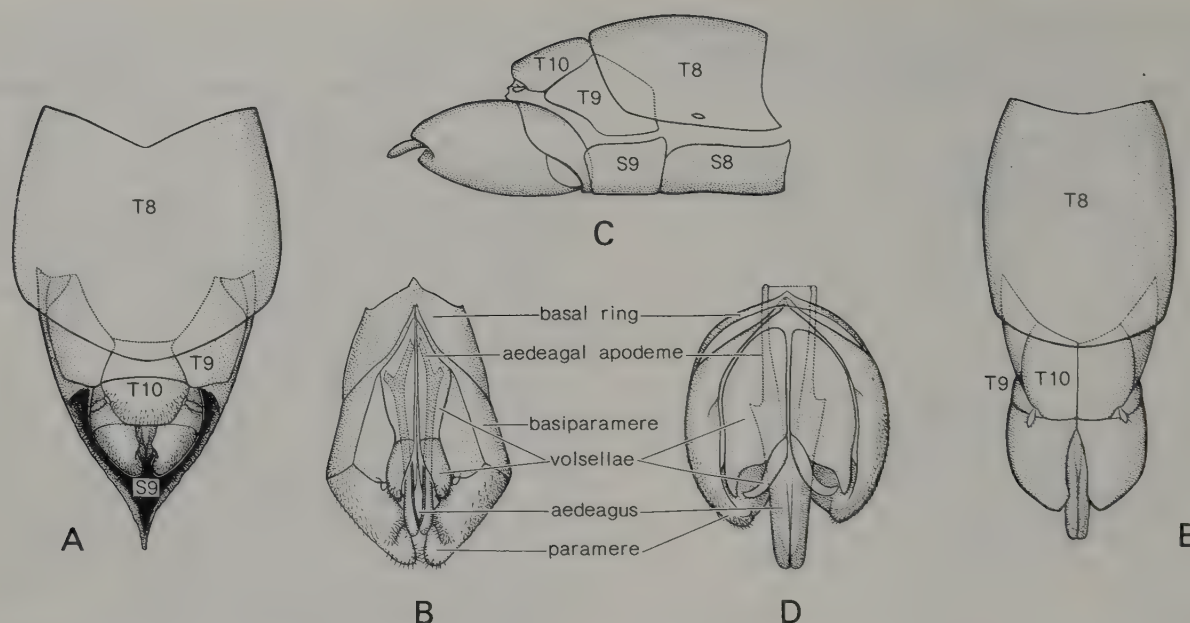


Fig. 42.11 Male terminalia: A, B, Symphyta (*Sirex noctilio*, Siricidae); C–E, Apocrita (*Rhyssa* sp., Ichneumonidae).

[S. Monteith]

the female during copulation; they often bear small teeth (*volsellar digitae*). The basal portion of each paramere is sometimes differentiated as a *basiparamere*. The basal ring, basiparameres and volsellae are derived from gonocoxites 9; the apical portion of each paramere from the gonostyle; and the aedeagus from gonapophyses 9 (E. L. Smith 1970a).

The ovipositor (Fig. 42.12) arises behind S7 (*hypopygium*) and consists of 3 valves and 2 major, basal sclerites. The *ventral valves* (anterior valves, valvulae 1, *stylets*) are the paired, movable parts of the ovipositor. The *medial valves* (valvulae 2) are fused to form a 2-railed track along which the ventral valves slide. There is sometimes a detached, forked sclerite (*furcula*) at the base of the medial valves. The *dorsal valves* form an *ovipositor sheath*. The ventral and medial valves together form the cutting or piercing organ (*terebra*); often they are sharply pointed and have at least a few minute, subapical teeth. The *anterior valvifer* (valvifer 1, gonangulum) and *posterior valvifer* (valvifer 2) form part of the basal mechanism.

The basic plan of the hymenopteran ovipositor is not markedly different from that of Archaeognatha. The ventral and medial valves are derived from gonapophyses 8 and 9 respectively, the dorsal valves from the gonostyle, and the anterior and posterior valvifers from gonocoxites 8 and 9 respectively (E. L. Smith 1970a). Oeser (1961), Copland *et al.* (1969–76) and Fergusson (1988) provide comparative and functional accounts.

The ovipositor is sometimes highly mobile, allowing the valves to be swung vertically or even anteriorly between the legs. In some Hymenoptera the valves are elongate while in others they are short, stabbing organs. Sensilla on the valves enable the female to recognise suitable oviposition sites. In aculeates the ovipositor forms a hypodermic needle to inject paralysing liquids. Females of parasitic Hymenoptera sometimes pierce the host with

the ovipositor and then turn to feed on the host's body fluids which provide protein for egg production. If the host is concealed within plant tissue or a cocoon, the ovipositor can be used as a mould for the construction of a drinking straw through which the host fluids can be imbibed.

**Internal Anatomy.** Alimentary system more or less uniform with oesophagus dilating into a thin-walled crop that serves as a reservoir ('honey-stomach') for imbibed fluids in Sphecoidea, Vespoidea and Apoidea. Proventriculus functions as a pump or filter. Protective peritrophic membrane absent in some liquid-feeders (e.g. adult ants). Malpighian tubules variable in number (6–250); usually more numerous in aculeates than in terebrants, moderate number in Symphyta, few in ants. Nervous system with 2–3 thoracic and 1–9 abdominal ganglia.

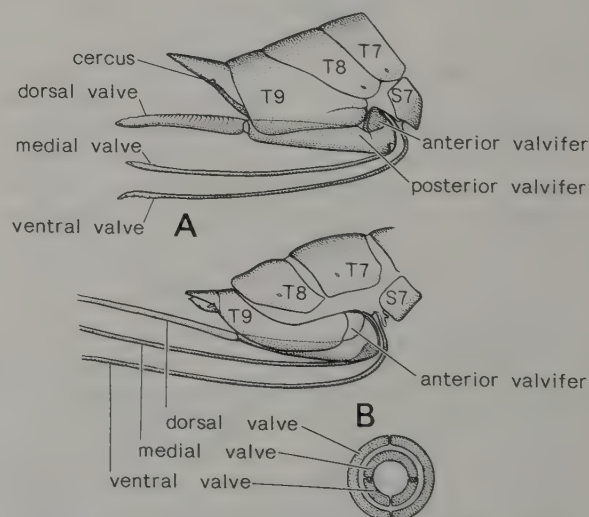


Fig. 42.12 Female terminalia: A, Symphyta (*Sirex noctilio*, Siricidae); B, Apocrita (*Rhyssa* sp., Ichneumonidae).

[S. Monteith]



'Mushroom bodies' in the brain appear to be larger, with greater surface area, in some aculeates with complex foraging behaviour, than in sawflies. Male with paired testes, seminal vesicles and large accessory glands; sometimes (e.g. in short-lived males of terebrants) spermatogenesis completed in pupa, and testes of adult small. Females with paired ovaries, each commonly with 3–5 polytrophic ovarioles (up to 180 ovarioles per ovary in *Apis mellifera*) and (usually) median spermatheca. In female Symphyta the accessory glands produce a protective covering for the eggs and lubricant for the ovipositor. In Apocrita these glands also or exclusively produce venom which is used to paralyse or kill hosts or prey, or assist in nest defence (Robertson 1968). Venoms are proteinaceous but include additional substances, e.g. formic acid in ants (Piek 1986). In some Apocrita components of the venom apparatus secrete host- or trail-marking chemicals or alarm pheromones.

### Immature Stages

**Egg** (Figs 42.14E, F). Usually ovoid or sausage-shaped; with respiratory stalk in some endoparasitic species; with hook- or sucker-like attachment devices in some ectoparasites. Chorion usually thin, smooth; sometimes tough, sculptured. Eggs of parasitic species sometimes with little yolk. Polyembryony, i.e. development of several individuals from one egg, occurs in *Copidosoma* (Encyrtidae) and a few Braconidae, Dryinidae and Platygasteridae; from 5 (e.g. Platygasteridae) to several thousand (*Copidosoma*) individuals can be produced from one yolk-deficient egg.

**Larva.** Head usually well developed. Eyes represented on each side by single-lensed stemma. Antennae either multisegmented or reduced to flat, membranous areas; never long. Frontoclypeal (epistomal) and clypeolateral sutures present or absent. Mandibles present, working in horizontal plane, labium sometimes with spinneret. Thoracic legs present or absent. Abdominal prolegs present or absent, without crochets. Abdomen with 10 segments. Body segmentation sometimes indistinct; with at most 10 spiracles (2 thoracic, 8 abdominal).

In Symphyta (Figs 42.13A–D) the larva is typically eruciform (caterpillar-like) with 3 pairs of thoracic legs (each leg usually with apical claw) and abdominal prolegs (commonly on segments 2–8 and 10). The thoracic and abdominal legs are reduced or absent in larvae feeding in mines or tunnels. The head capsule is usually sclerotised, pigmented and with a pair of stemmata, 1–7-segmented antennae, broad mandibles and prominent maxillae and labium with segmented palps.

In Apocrita (Figs 42.13E–J) the larva is apodous. The head capsule is more weakly sclerotised than in Symphyta and sometimes retracted into the prothorax. Stemmata are absent and the antennae are represented by membranous areas or sensory papillae. The mandibles are strongly sclerotised, sometimes spine-like, sometimes broad with numerous teeth. The maxillae and labium are often reduced to fleshy lobes with the palps no more than small papillae. A framework of sclerites is often associated with the mouth-parts. Spiracles are usually present on

the prothorax and abdominal segments 1–8. In most the mid gut is closed posteriorly until the final instar; just prior to pupation the mid and hind gut become continuous and the larva defaecates.

Larval heteromorphosis occurs in many parasitic species. In these, whereas the final instar is *hymenopteriform* (i.e. body spherical to spindle-shaped, 12- or 13-segmented), the 1st or intermediate instars are of diverse form. Larval types include: (1) the active *planidium* (triungulin-like but with spine-like locomotory processes instead of legs, Fig. 42.14A; e.g. Leucospidae, Perilampidae, Eucharitidae); (2) the *teleaform type* (distinctly segmented, apical abdominal segment forming a fleshy tail; e.g. Scelionidae); (3) the *cyclopoid type* (cephalothorax larger than abdomen, mandibles very large and falcate, Fig. 42.14C; e.g. Platygasteridae); (4) the *caudate type* (distinctly segmented, apical abdominal segment forming a fleshy tail, Fig. 42.14B; e.g. many Ichneumonidae, Braconidae, some Proctotrupoidea); (5) *vesiculate type* (hymenopteriform but with hind gut invaginated to form an external vesicle, Fig. 42.14D; e.g. some Braconidae, Ichneumonidae, Encyrtidae); (6) the *microtype* (minute, segmented, with strong spines or hooks; e.g. Trigonalidae); (7) the *eucoiliform type* (thoracic segments with long, fleshy processes and abdomen tapered, often forming a tail; e.g. many Cynipoidea); (8) the *polypodeiform type* (body cylindrical, segments with fleshy, ventral lobes; e.g. some Braconidae, Cynipoidea and Proctotrupoidea); (9) the *sacciform type* (bag-like, unsegmented; e.g. some Dryinidae, Trichogrammatidae, Mymaridae); (10) the *encyrtiform type* (body segmented, with posterior spiracles and these on a stalk; e.g. many Encyrtidae); (11) the *mymariform type* (body very elongate, indistinctly segmented except for head and tail-like apical segment; e.g. some Mymaridae, Trichogrammatidae); (12) the *mandibulate type* (head very large with falcate mandibles; e.g. many Ichneumonidae, Braconidae, Proctotrupidae, Diapriidae, 3rd instar Trigonalidae).

**Pupa.** Aedeicous; usually exarate, more or less obiect in Chalcidoidea. Cocoon spun with silk from labial glands; sometimes flimsy or reduced to a lining of the larval cell; absent in most Chalcidoidea and Cynipoidea, and some Apoidea and Formicidae.

### Biology

**Adults.** Hymenoptera are almost ubiquitous and occur in soil and litter, on vegetation (especially flowers), flying actively or drifting in air currents, drinking or gathering mud at the edges of water or nesting in man-made environments. A few parasitise eggs of aquatic insects and swim in fresh water. Strand dwellers hunt and nest just above high tide levels. There is an ant associated with coral but generally marine and frigid environments are devoid of Hymenoptera.

Adults feed mostly on nectar or honeydew. A few extralimital sawflies prey on other small insects, females of many parasitic Apocrita imbibe host body fluids, and some nest-building aculeates consume portions (especially haemolymph) of the insects with which they feed their offspring.

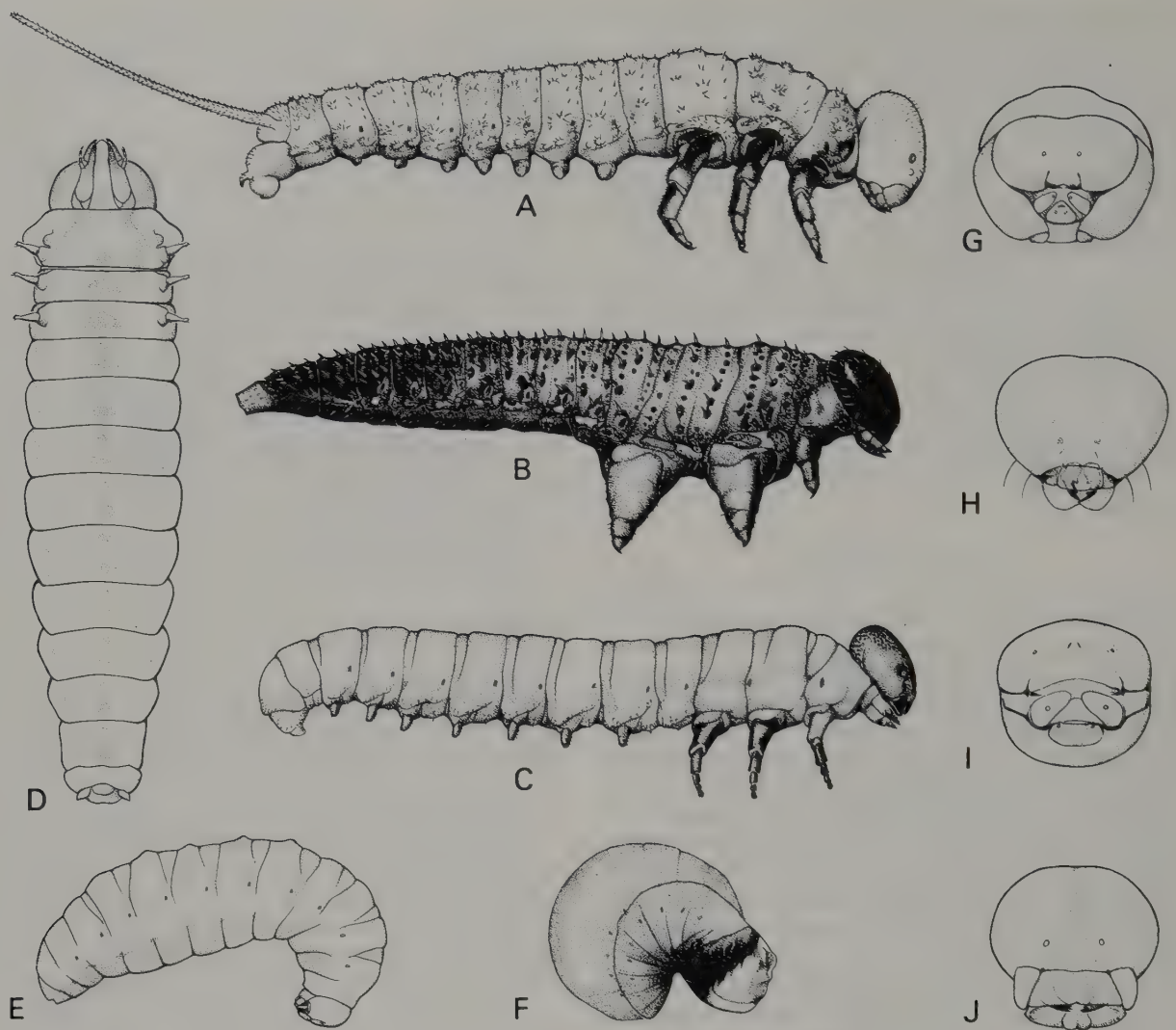


Fig. 42.13 Larvae: A–D, Symphyta, E–J, Apocrita: A, *Philomastix* sp., Pergidae–Philomastiginae; B, *Perga* sp., Pergidae–Perginae; C, *Zenarge turneri*, Argidae; D, *Phylacteophaga* sp., Pergidae–Phylacteophaginae; E, *Paralastor* sp., Vespidae; F, unidentified Dryinidae. Heads, frontal: G, *Myrmecomimesis* sp., Chrysididae; H, unidentified Platygasteridae; I, *Westwoodia* sp., Ichneumonidae; J, *Taeniogonalos* sp., Trigonalyidae. [S. Monteith]

Females of a few Apocrita which oviposit in eggs of other insects are phoretic on adults of the host species. The female wasps leave the adult insect and attack freshly laid egg masses. *Mantibaria anomala* (Scelionidae), which is phoretic on mantids, feeds on mantid haemolymph while it is attached.

Most Hymenoptera are diurnal or crepuscular. A few parasitic wasps attack hosts which are accessible only at night; such night-active wasps commonly are of distinctive, 'ophionoid' appearance with pale coloration and large compound eyes and ocelli. Some ants and a few tropical, non-Australian Pompilidae, Vespinae and Polistinae are among the few nocturnal, predatory Hymenoptera. Some diurnal, solitary-nesting wasps and bees form 'sleeping' aggregations on plants or in the ground, but the function of these nocturnal aggregations is unclear.

Adult Hymenoptera are among the most important of

pollinators (Armstrong 1979). The role of bees is well known but sawflies (especially Pergidae), Scoliidae, Tiphidae, Vespidae, Pompilidae and Chrysididae all commonly visit flowers and many have been observed with pollinia on their legs. Males of Thynninae (Tiphidae) and *Lissopimpla excelsa* (Ichneumonidae) are attracted to flowers of various terrestrial orchids. The flowers mimic female wasps in odour and/or appearance; male wasps attempt to copulate with the flowers and in doing so transfer pollen. Agaoninae (Agaonidae) are essential, species-specific pollinators of figs.

Stridulation appears to be widespread within the order. In some Perginae (Pergidae) the rubbing of a modified area of the fore wing over the cenchri produces an audible sound, and in ants and mutillids various files and scrapers on overlapping metasomal terga can be dragged over each other to the same effect. Sound production is clearly defensive behaviour in some species and may be impor-



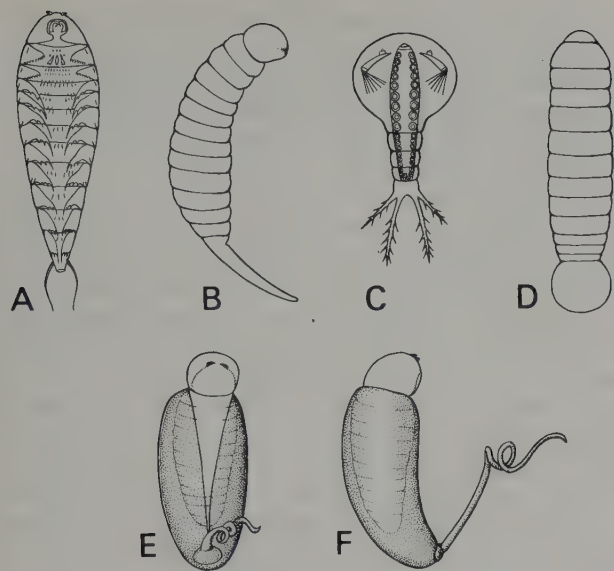


Fig. 42.14 A–D, heteromorphic larvae of Apocrita: A, planidium; B, caudate type; C, cyclopoid type; D, vesiculate type; E, F, egg of *Netelia* sp., Ichneumonidae.

[A–C after Clausen 1940; D after Richards and Davies 1977; E, F by S. Monteith]

tant in intraspecific communication in others. Mud-dauber wasps buzz loudly when gathering mud and during nest building and it has been suggested that the resulting vibrations help to compact the mud.

Many adult Hymenoptera are distasteful to vertebrate predators or capable of defending themselves with their sting. Aposematic colour patterns are of widespread occurrence (e.g. in Apoidea, Vespidae, Pompilidae), and wasps and ants are frequently models in mimicry complexes. In many parasitic species which frequent tree trunks wing banding heightens resemblances to ants. A North Qld *Cerceris* (Sphecidae) mimics a common, aggressive, social vespid.

Most commonly, males are polygamous and females monandrous, although *Apis mellifera* is a notable exception.

In orthandrous Symphyta the male genitalia have the normal orientation; the male mounts the female and, while the two are facing in the same direction, curves the tip of his abdomen around the tip of hers. In strophandrous Symphyta the male genitalia are twisted through 180° and male and female copulate facing in opposite directions, with their bodies in a straight line.

Generally courtship in Apocrita is more complex and involves sequences of antennal contact, leg and wing vibrations, mandibular movements and pheromones (e.g. Gordh and DeBach 1978; van den Assem *et al.* 1982). The male mounts the female as in orthandrous Symphyta. In many species males are much smaller than females and cannot simultaneously maintain contact with the female's head and antennae and copulate. After initial courtship involving interplay of the antennae, the female signals receptivity and the male moves more posteriorly to copulate.

Males of parasitic species most commonly search for

females at emergence sites and occasionally fight for possession of such sites. Males of nest-building aculeates patrol emergence sites, flowers or landmarks such as prominent plants, in search of females (Alcock *et al.* 1978). Males of some establish territories (commonly of 1–5 m<sup>2</sup> and encompassing potential emergence sites) and defend these territories against conspecific males. In a few cases, other animals (other wasps, bees, dragonflies, birds) or even inanimate objects are pursued or pounced upon by these territorial males. Males of some extralimital Anthophoridae excavate virgin females from nests in the ground and males of some parasitic Apocrita chew into cocoons and mate with pre-emergent females. Males of some Neotropical Euglossinae (Apidae) form female-attracting swarms. Female Thynninae (Tiphidae) attract males by releasing a pheromone and assuming an immobile, head-down posture on vegetation.

Phoretic copulation is usual in many groups of wasps in which the female is wingless, e.g. Thynninae, some Bethyidae and Mutillidae (H. E. Evans 1969b). In thynnines the male genitalia rotate during copulation so that either both male and female are dorsum-up and facing in opposite directions, or the female is curled under the male so that the two are venter-to-venter, forming a C-shape. Phoretic coupling is particularly prolonged in thynnines and the males, which are larger than the females, carry their partners to feeding sites; males sometimes feed females by regurgitation or from a food bolus formed in a seta-fringed concavity beneath the head.

**Reproduction.** Males of Hymenoptera (with very rare exceptions) are haploid and females diploid (*haplodiploidy*). Parthenogenesis is universal (Slobodchikoff and Daly 1971) and three types are recognised: *arrhenotoky* (uninseminated females deposit haploid eggs only; inseminated females deposit both haploid and diploid eggs); *thelytoky* (males rare or absent; parthenogenesis achieved, for example, by the absence of meiosis); and *deuterotoky* (unfertilised females produce eggs of both sexes). Arrhenotoky is most common; thelytoky occurs in Australian *Caliroa cerasi* (Tenthredinidae) and many Chalcidoidea; and some Pergidae are deuterotokous.

Females of biparental species store sperm in the spermatheca and release this sperm into the oviduct in response to environmental factors such as host abundance. Thus females determine the sex of their offspring and can manipulate the rate of increase of their populations.

Hymenoptera are well able to maintain their reproductive capacity when environmental conditions are unfavourable. Many parasitic species produce only 'hydropic' eggs, i.e. eggs with little yolk; these can be stored in the uterus since they will not develop further until they are able to obtain nourishment from the body fluids of a host. Small, hydropic eggs pass quickly down the ovipositor, allowing rapid oviposition. Some species produce yolk-replete ('anhydropic') eggs but such eggs cannot be retained for long in the uterus; because Hymenoptera are parthenogenetic development may begin and result in the egg becoming too large to pass down the lumen of the ovipositor. If the female is unable

to oviposit, yolk-replete eggs are resorbed before they enter the oviduct. Resorption of eggs can prolong the life of non-ovipositing females. The large, well-developed eggs of Tryphoninae (Ichneumonidae) are sometimes retained temporarily outside the reproductive tract, at the base or at the tip of the ovipositor; the larvae may split the chorion of the eggs but do not emerge until after oviposition.

Relatively large, yolk-replete eggs must be compressed to some degree as they move down the ovipositor and yolk is sometimes squeezed from the body of the egg into a thin, chorionic tail. It is said that large eggs tend to travel slowly, which prolongs each act of oviposition.

In Apocrita in which the ovipositor is modified to form a sting, the eggs are deposited directly from the genital opening and do not pass down the ovipositor.

**Life Histories.** Four groups of Hymenoptera can be recognised on the basis of larval feeding habits: (1) the predominantly phytophagous Symphyta; (2) Apocrita which are parasitic or feed in plant galls; (3) non-social Apocrita, larvae of which are fed with prey (predatory species) or pollen and nectar (melliferous species); and (4) the social (eusocial) Apocrita. Only some Symphyta larvae and a very few larvae of Apocrita are obliged to search for food for themselves. In the majority of life cycles males emerge before females.

(1) Symphyta oviposit either in leaves (most species), in stems (some extralimital species), in wood or (more rarely) in leaf litter, and females sometimes stand guard over their egg masses. Their larvae are almost exclusively phytophagous, feeding externally or in mines, tunnels or galls. Species commonly attack a wide range of related plants. Some larvae feed or shelter gregariously. Most siricoid larvae tunnel in wood but are unable to digest this and depend on symbiotic fungi to break down the woody tissue. Some Euryinae (Pergidae) specialise on dead leaves and their larvae are most common in forest litter. Orussidae are unusual in being parasitic on xylophagous larvae. Symphyta pupate either within the plant tissue in which they have been feeding or in the ground.

(2) Parasitic (or parasitoid, as they are sometimes termed) habits are widespread within the Apocrita. The adult wasp is free living and it is the larva which is closely associated with the host (i.e. *protelean parasitism*). *Idiobionts* prevent any further development of the host after initial parasitisation. *Koinobionts* allow the host to continue its development and often do not kill and consume the host until the host has reached its maximum size. Some parasites appear to induce premature metamorphosis by the host, others retard development (Jones 1985; M. R. Shaw 1983). The larvae of some parasites are capable of moving small distances from one host to another, e.g. from one egg to another in an egg mass or from one host cell to the next.

Eggs usually are laid on, in or near to the host and larvae feed either externally or internally. Sometimes early instars are endoparasitic and later instars ectoparasitic. Pupation usually occurs either within or beside the host remains.

Some parasites oviposit on vegetation frequented by

potential hosts. The mobile 1st instar larva of the parasite locates and attaches to the hosts. First instar eucharitid larvae attach themselves to worker ants and are carried to the nest where they transfer themselves to ant immatures. The eggs of trigonalysids are inserted in leaves and are ingested by the caterpillars or sawflies in which they develop.

Hyperparasitism (i.e. the development of a secondary parasite or hyperparasite at the expense of a primary parasite) is more frequent in Hymenoptera than in any other order (Sullivan 1987) and the most common primary parasites exploited are parasitic Hymenoptera and Diptera. In some cases the female hyperparasite oviposits speculatively and her progeny develop only if the host is attacked subsequently by a primary parasite. In other cases the female hyperparasite can detect hosts which already have a primary parasite, or the female attacks only after the primary parasite has destroyed the primary host. Some species can complete their larval development either as primary parasites or as hyperparasites.

Solitary parasitism, i.e. the development of one parasite per host, is obligatory for many species. If more than one egg is laid per host, supernumerary larvae are killed by fighting or oxygen starvation. Sensory organs on the ovipositor enable adult females to recognise parasitised hosts and avoid such wasteful superparasitisation. Some parasites chemically mark the exterior of hosts in which they have oviposited.

Parasite larvae which develop gregariously are not aggressive to each other, but if the total food supply is small some may starve or the resulting adults may be undersized.

Within the parasitic Apocrita host-specificity varies greatly. Females of some species will oviposit on a range of broadly similar hosts which occur in a particular habitat. Such generalists often have an even greater potential host range. Other parasitic species are highly specific, e.g. to one host or to a few closely related species. These specialists tend not to be able to develop on other hosts even under extraordinary or artificial conditions. Nutritional factors, host defence mechanisms and the impediments to emergence presented by the host cocoon or feeding shelter, all can influence host suitability.

The life cycles of some terebrant Apocrita are similar to those of parasitic species except that females oviposit in plant tissue, galls are induced, and the wasp larva is phytophagous.

(3) Predatory species oviposit on or close to the paralysed prey. The transition from parasitic to predatory habits is illustrated by Pompilidae and Sphecidae. The most primitive pompilids sting a single spider, oviposit on it and depart; the spider recovers and lives actively for some time, until succumbing to the pompilid larva. In more advanced Pompilidae and primitive Sphecidae a single host is immobilised in its own retreat or concealed in a pre-existing niche located by the wasp. More advanced pompilids and sphecids excavate a nest before locating prey. Large, multicelled nests in which each cell is stocked with many, small prey, are characteristic of many behaviourally advanced species. Most predatory



Hymenoptera are *solitary* (i.e. each female makes her nest without the co-operation of others).

*Mass provisioners* fill each cell with sufficient prey for larval development and then seal the cell. *Progressive provisioners* (many Sphecidae and Vespidae) provide additional food at intervals. Most wasps provision with intact hosts but some Pompilidae amputate legs of prey for ease of carriage and storage, and some Vespidae masticate food for their larvae. Most predators will provision with a range of similar prey occurring in a particular habitat and few are highly specific or extremely polyphagous. Females walk or fly to their nests, gripping prey usually with the mandibles or legs, but sometimes carrying prey in specialised metasomal modifications or impaled on the ovipositor.

*Fossorial* species nest in the ground. Others occupy pre-existing cavities (especially in wood) or excavate the pith from stems. Free nests of mud or plant fibres are constructed by representatives of several families. Many species reoccupy abandoned nests of other Hymenoptera and remodel them with mud, resin or silk. Sealed cells usually have some internal asymmetry which determines the direction by which the emerging wasp or bee will escape. This ensures that the insect takes the easiest route to the outside or the route least destructive of neighbouring cells.

Nesting Hymenoptera memorise salient features of the terrain surrounding their nests and locate entrances using nearby landmarks.

Bees (most of which are solitary nesters) and Masarinae (Vespidae) are similar to predatory wasps except that they provision larval cells with pollen and nectar rather than arthropod prey.

*Cleptoparasites* construct no nests of their own and develop primarily on the food stores of other wasps and bees.

(4) Social Hymenoptera usually feed their larvae progressively. The food is diverse, e.g. material of animal origin supplemented with nectar in vespids; pollen and nectar sometimes supplemented with glandular secretions in bees; animal prey, nectar, seeds or fungi in ants; non-viable *trophic* eggs in some bees and ants.

Nests are founded either by one fertile female or by several conspecific individuals. Individuals co-operate in caring for the immature stages. There is a division of reproductive labour with one or more females (sometimes termed 'queens') laying eggs, and some individuals making up an at least temporarily sterile worker class, and successive generations overlap. Highly developed chemical communication regulates colony life. Colony defence has high priority and there may be a morphologically recognisable soldier class. Many species are territorial and aggressive to conspecifics from adjacent nests. Foragers are skilled navigators, making use of trail-marking chemicals and polarised light as well as terrain memory. The large and complex nests of some social Hymenoptera reflect co-operative building and long occupancy, but nests of some others are small and simple, and some army ants form only exposed, temporary bivouacs during nomadic phases in their life.

Among the Australian Sphecidae and Halictidae there are several species which nest communally and represent intermediate stages between solitary and true social behaviour.

The queens of *social parasites* usurp the position of the queens of host colonies. Host workers accept the foreign queen and care for her offspring.

**Natural Enemies.** Climatic factors and the availability of food, hosts and nesting sites generally determine the abundance of Hymenoptera. However, natural enemies are numerous. Many parasitic and cleptoparasitic Hymenoptera, Coleoptera (Rhipiphoridae, Meloidae) and Diptera (Tachinidae, Bombyliidae, Calliphoridae-Miltogrammatinae) develop at the expense of immature Hymenoptera, especially those in nests. Hyperparasitic wasps cause significant mortality among parasitic species. Ants and predatory wasps prey on both adults and immatures of other Hymenoptera. Stylopisation and nematode infections cause partial or complete sterility. Stylopisation is restricted to Vespidae, Apoidea, Sphecidae and Formicidae, and the percentage parasitisation usually is low, but nematode infections (e.g. in *Sirex noctilio*, Vespidae or Apoidea) sometimes drastically depress the numbers of their host population. Parasitic mites are associated with some Vespoidea and Apoidea. Fungal, bacterial, viral and protozoan pathogens are often important, especially in social Hymenoptera. Opportunist predators on Hymenoptera include some Hemiptera, Neuroptera, spiders, frogs, reptiles, birds and mammals. Ants are an important dietary item for several vertebrate species.

**Economic Significance.** No insects are more beneficial than are the Hymenoptera. The many parasitic and predatory species are of major importance in regulating the abundance of other arthropods, including many pests. Bees are important or essential pollinators of forest and orchard trees, of vegetables and of pasture crops such as lucerne. Additionally, *Apis mellifera* is of great commercial value as a producer of honey.

Few Hymenoptera are harmful. Leaf-feeding sawfly larvae (Pergidae, Tenthredinidae, Argidae) sometimes damage forest, orchard or ornamental trees, but tree death is uncommon. Wood-boring larvae of *Sirex noctilio* (Siricidae), in association with fungi, can cause extensive damage to plantations of introduced pine trees. *Bruchophagus* (Eurytomidae) causes stem galls on *Citrus* and destroys lucerne seed. Some parasitic wasps attack hosts which are useful to man and a few, as hyperparasites, reduce the beneficial effects of primary parasites. A few ants are pests, e.g. in homes or as seed harvesters, and some protect sap-sucking insects which are themselves pests. Nest-building Hymenoptera, including the introduced *Vespula* spp. (Vespidae), can be domestic nuisances and, through their stinging, a minor health hazard to humans.

### Special Features of the Australian Fauna

The Hymenoptera include many strong-flying species and many forms which are dispersed readily by air currents. Thus, it is not surprising that many species and higher taxa are shared by Australia and adjacent regions. Only

three families (Peradeniidae, Austroniidae and Stenotritidae) and about 8% of the subfamilies are endemic. However, at the generic and specific level the fauna is more distinctively Australian, especially among groups characteristic of arid regions and moist, temperate forests. The moist tropical forests of the north-east share many faunal elements with the Oriental and Melanesian regions.

The families of Symphyta are poorly represented and Pergidae predominate. Larvae of most Australian Symphyta feed externally on plants and only the few Siricoidea (which develop in wood), the endemic, leaf-mining Phylacteophaginae (Pergidae) and an introduced, leaf-mining argid have concealed larvae. Generally Symphyta are more numerous in temperate regions.

From the Apocrita the gall-forming Cynipidae are a notable absence. In Australia the gall-forming niche has been filled largely by Chalcidoidea, especially Pteromalidae, Torymidae, Eurytomidae and Eulophidae.

Several apparently very primitive families or subfamilies of Symphyta and Apocrita (Xiphydriidae-Xiphydriinae, Stephanidae, Trigonalidae, Megalynidae, Aulacidae) which have an almost relict distribution world-wide, are well represented in Australia. Australian representatives of many relatively archaic families and subfamilies have their closest affinities with the South

American fauna, e.g. Xiphydriidae-Derycyrtinae, Pergidae-Philomastiginae, Orussidae, Gasteruptiidae-Hyptiogastrinae, Ichneumonidae-Labeninae, Monomachidae, Diapriidae-Ambositrinae, Tiphidae-Thynninae, Pompilidae-Epipompilinae. These Gondwanan elements tend to be more common in moist, temperate regions.

The Australian, dry-temperate bee fauna is highly distinctive, with the Colletidae pre-eminent and largely dependent on Myrtaceae. Bees (as well as many of the nest-building, larger wasps) are much less diverse in very wet forests and the coolest regions.

Parasites of insect larvae feeding in concealed situations such as in leaf mines or rolls are particularly diverse (e.g. some Eulophidae, cremastine Ichneumonidae), which reflects possibly the diversity of these cryptic hosts in the relatively arid Australian environment.

The Australian ants include many old endemic genera, particularly in the southern areas, and a number of endemic lineages are derived from these. However, many ant genera clearly have entered Australia from the Indo-Oriental region, particularly via New Guinea and Cape York. The Australian ant fauna is rich at the generic level, with about as many genera as the Neotropical region. Many genera are very species-rich, perhaps more so than is usual on other continents, and possibly the continental species tally will be the largest in the world.

## CLASSIFICATION

### Order HYMENOPTERA

(14 781 Australian spp.)

#### Suborder SYMPHYTA (176)

##### XYELOIDEA (0)

Xyelidae (0)

##### MEGALODONTOIDEA (0)

Megalodontidae (0)

Pamphiliidae (0)

##### CEPHOIDEA (0)

Cephidae (0)

##### SIRICOIDEA (19)

Anaxyelidae (0)

1. Xiphydriidae (7)

2. Siricidae (1)

3. Orussidae (11)

##### TENTHREDINOIDEA (157)

4. Tenthredinidae (4)

5. Argidae (13)

Blasticotomidae (0)

Cimbicidae (0)

Diprionidae (0)

6. Pergidae (140)

#### Suborder APOCRITA (14605)

##### STEPHANOIDEA (7)

7. Stephanidae (7)

##### TRIGONALYOIDEA (13)

8. Trigonalidae (13)

##### MEGALYROIDEA (25)

9. Megalynidae (25)

##### CERAPHRONOIDEA (100)

10. Ceraphronidae (60)

11. Megaspilidae (40)

##### EVANIOIDEA (233)

12. Evaniidae (40)

13. Aulacidae (31)

14. Gasteruptiidae (162)

##### ICHNEUMONOIDEA (2044)

15. Ichneumonidae (1244)

16. Braconidae (800)

Apozygidae (0)

##### PROCTOTRUPOIDEA (374)

17. Monomachidae (3)

18. Diapriidae (325)

19. Heloridae (1)

20. Peradeniidae (2)

21. Austroniidae (3)

22. Proctotrupidae (40)

Vanhorniidae (0)

Pelecinidae (0)

Roproniidae (0)

##### PLATYGASTEROIDEA (545)

23. Platygasteridae (100)

24. Scelionidae (445)

##### CYNIPOIDEA (69)

25. Ibaliidae (2)

26. Liopteridae (2)

27. Figitidae (3)

28. Cynipidae (10)

29. Charipidae (12)

30. Eucoilidae (40)

##### CHALCIDOIDEA (3646)

31. Mymaromatidae (3)

32. Chalcididae (250)

33. Leucospidae (11)

34. Eurytomidae (150)

35. Torymidae (215)

36. Ormyridae (9)

37. Agaonidae (50)

38. Pteromalidae (525)

39. Perilampidae (65)

40. Eucharitidae (97)

41. Eupelmidae (177)

42. Tanaostigmatidae (8)

43. Encyrtidae (600)

44. Aphelinidae (250)

45. Signiphoridae (10)

46. Tetracampidae (6)



Rotoitidae (0)	VESPOIDEA (4878)	APOIDEA (1652)
47. Eulophidae (750)	Sapygidae (0)	65. Colletidae (860)
48. Elasmidae (60)	Sierolomorphidae (0)	66. Stenotritidae (30)
49. Trichogrammatidae (140)	Bradynobaenidae (0)	67. Halictidae (382)
50. Mymaridae (270)	57. Rhopalosomatidae (3)	Andrenidae (0)
CHRYSIDOIDEA (275)	58. Pompilidae (231)	Melittidae (0)
Plumariidae (0)	59. Mutillidae (500)	Oxaeidae (0)
51. Scolebythidae (2)	60. Tiphidae (750)	68. Ctenoplectridae (1)
52. Sclerogibbidae (3)	61. Scoliidae (25)	69. Megachilidae (171)
53. Embolemidae (4)	62. Vespidae (369)	70. Anthophoridae (194)
54. Dryinidae (90)	63. Formicidae (3000)	71. Apidae (14)
55. Bethyidae (100)	SPHECOIDEA (744)	
56. Chrysididae (76)	64. Sphecidae (744)	

### KEY TO THE SUBORDERS OF HYMENOPTERA

- Mid and posterior tagmata broadly joined (e.g. Figs 42.1A, 16); wings with numerous closed cells (e.g. Figs 42.1A, 8A, 16) [except in apterous *Cladomacra* (Pergidae) from New Guinea and the Oriental region]; fore tibia usually with 2 apical spurs; cenchri (Fig. 42.6A) present (except in extralimital Cephidae). Larva with segmented legs (Figs 42.13A–D) except in a few tunnelling and leaf-mining species; antenna and maxillary and labial palps all with several segments, or, if 1-segmented, then apex of abdomen with median sclerotised process or legs indicated by sclerotised discs ..... SYMPHYTA (p. 931)
- Mid and posterior tagmata usually separated by distinct constriction (e.g. Figs 42.1B, 17); if constriction absent (e.g. Fig. 42.28D) either abdomen with T1 incorporated into thorax and with wing venation very reduced (e.g. Figs 42.27j, 28A) or wings absent (Fig. 42.23F); fore tibia usually with 1 apical spur; cenchri absent. Larva apodous (Figs 42.13E–J); antenna and maxillary and labial palps 1-segmented or absent; apex of abdomen not sclerotised ..... APOCRITA (p. 935)

In their adult and larval morphology Symphyta retain many features plesiomorphic within the Hymenoptera. The less specialised of the sawflies have the most complete wing venation seen within the order and all sawflies retain the typical hexapod tagmosis. The Apocrita are derived from the Symphyta, probably as a sister group of the Siricoidea or the Cephoidae, and thus the Symphyta are a paraphyletic assemblage. Apocrita generally have more modified or reduced venation and specialised tagmosis. Presumably the 'wasp waist', which is almost diagnostic of Apocrita, was an evolutionary innovation associated with the more effective use of the ovipositor. The waist allows considerable mobility of the most posterior body tagma (the metasoma) and pre-adapts species for stinging and/or ovipositing on arthropod hosts or prey.

#### Suborder SYMPHYTA

Adults without a marked constriction between abdominal segments 1 and 2 (e.g. Fig. 42.1A; slight constriction evident in Orussidae and the extralimital Cephidae). Metanotum with a pair of very finely sculptured protuberances (cenchri, Fig. 42.6A) which engage a 'scaly patch' of microtrichia in the anal region of the fore wing and fasten the folded wings to the body. Possibly in Pergidae the cenchri are stridulatory organs with the nearby piliferous lobes acting as resonators (Riek 1970). Cenchri are absent in Cephidae. The ovipositor is saw-like in most families, sword-like in most Siricoidea, and filamentous in Orussidae. Larvae of Symphyta are usually eruciform, with a well-developed head capsule, thoracic legs and abdominal prolegs (Figs 42.13A–D). The thoracic and abdominal segments are often annulated. The legs are

reduced or absent in many larvae feeding in tunnels or leaf mines.

The most primitive symphytan probably was morphologically very similar to extant, extralimital Xyelidae, with larvae feeding inside the mature cones of gymnosperms. Modern xyelids (some of which feed on angiosperms) occur only in the Holarctic region but the family was more widespread in the Mesozoic and extinct genera from the Triassic of south-eastern Qld and the U.S.S.R. are the earliest fossil records of the Hymenoptera.

From this xyelid-like ancestor two lineages arose. One gave rise to the Tenthredinoidea, all families of which (except the extralimital Blasticotomidae) are strophandrous (i.e. the male genitalia are rotated 180° prior to eclosion). The second lineage, in which the male genitalia are orthandrous (i.e. not rotated) gave rise to the remaining symphytan superfamilies (the so-called 'cryptozoic' Symphyta, the larvae of which lead a more-or-less concealed life) and the Apocrita. Possibly Megalodontoidea and Cephoidae were successive early branches from this second lineage. Several thoracic characters, especially of the prepectus, postspiracular sclerite, spiracle cover-lobe and transscutal articulation, indicate that the sister group relationships within the Siricoidea are Anaxyelidae + (Siricidae + (Xiphydriidae + (Orussidae + Apocrita))) which makes the Siricoidea paraphyletic (Gibson 1985; Rasnitsyn 1988).

Larvae of Symphyta are almost exclusively phytophagous, either as exposed feeders on foliage, or as concealed feeders in leaf mines or tunnels in stems or wood. Only Orussidae are parasitic. In Australia symphy-

tan larvae are sometimes conspicuous on trees and shrubs, but adults are seen less commonly. Megalodontoidea, with larvae feeding under webs in slits in conifer needles or in leaf rolls, and Cephoidea, with stem-boring larvae, are restricted mainly to the Northern Hemisphere.

The higher classification of Symphyta has been

reviewed by H. H. Ross (1937) and Benson (1938b), and by Rasnitsyn (1988) who included fossil taxa. Quinlan and Gauld (1981) and D. R. Smith (1988) gave keys and diagnoses to British and Neotropical families respectively. A survey of symphytan larvae by Smith and Middlekauff (1987) emphasised Northern Hemisphere forms.

### Key to the Families of Symphyta Known in Australia

1. Antennae inserted low on head, close to oral margin (Fig. 42.16j); hind wing without cross-veins *r-m* or *m-cu*; head with rasp-like tubercles lateral and dorsal to anterior ocellus (Fig. 42.3b) ..... **Orussidae** (p. 932)
- Antennae inserted well above oral margin (Figs 42.16a–i, k); hind wing usually with cross-veins *r-m* and *m-cu*; head without rasp-like tubercles lateral and dorsal to anterior ocellus ..... 2
- 2(1). Neck long with cervical sclerites (propleura), in lateral view, longer than high (Fig. 42.16k) ..... **Xiphydriidae** (p. 932)
- Neck short with cervical sclerites (propleura), in lateral view, not longer than high (Figs 42.16a–i) ..... 3
- 3(2). Fore wing cell 1R1 not contiguous with cell 1M (Fig. 42.16i); ovipositor projecting strongly beyond apical abdominal tergum; apical tergum (♀) or sternum (♂) with horn-like projection ..... **Siricidae** (p. 932)
- Fore wing cell 1R1 contiguous with cell 1M (Figs 42.16a–h); ovipositor not projecting strongly beyond apical abdominal tergum; apical segment without horn-like projection ..... 4
- 4(2). Radial cell of fore wing crossed by vein (Fig. 42.16h) ..... **Tenthredinidae** (p. 934)
- Radial cell of fore wing not crossed by vein (Figs 42.16a–g) ..... 5
- 5(4). Antennae 3-segmented, apical segment very long (Fig. 42.16g) and sometimes bifid ..... **Argidae** (p. 934)
- Antennae with more than 3 segments, apical segment not unusually long (Figs 42.16a–f) ..... **Pergidae** (p. 934)

### Superfamily SIRICOIDEA

Adult head with postgenal bridge and usually with subantennal groove; mesonotum usually with transverse suture or groove and axillae defined (Fig. 42.15A). Larva with very reduced thoracic legs which lack claws; without stemmata or abdominal prolegs; abdominal segment 10 sometimes with stout stiff process.

The subantennal groove and transverse mesonotal suture are absent in the western Nearctic *Syntexis libocedrii*, the only extant member of the Anaxyelidae.

Larvae develop in wood where many are associated with symbiotic fungi. Mature larvae pupate in the larval tunnels. Xiphydriidae and Siricidae are phytophagous and closely related, but the Orussidae, with reduced wing venation, an elongate ovipositor and parasitic, apocritan-like larva, are sometimes placed in a separate superfamily.

**1. Xiphydriidae** (Fig. 42.16k). Adult 3.5–14 mm; antennae filiform, 11–27-segmented; postgenal bridge complete; neck (propleura) elongate; fore wing cell 1R1 broadly contiguous with cell 1M; apical abdominal segment without horn-like projection; ovipositor strongly exerted. Larva with reduced, lobe-like thoracic legs and 3- or 4-segmented antennae; abdominal segment 10 with suranal process.

In the Northern Hemisphere xiphydriids develop in the wood of angiosperms, usually in dead or dying smaller branches. Larvae depend on symbiotic fungi in their tunnels and pupate after about a year.

DERYCYRTINAE, in which the mesoscutellum is tuberculate posteriorly, occur only in Australia (*Austrocyrtia*; 1 sp.) and South America. XIPHYDRIINAE are Holarctic and Indo-Australian. *Rhysacephala* (6 spp.) also occurs in New Guinea and on Aru I. [Riek 1955f; D. R. Smith 1978, 1988]

**2. Siricidae** (Fig. 42.16i). Adult 10–55 mm; antennae

filiform or flattened, 14–30-segmented; postgenal bridge separates oral cavity and foramen magnum; neck (propleura) short; fore wing cell 1R1 not reaching cell 1M or the two cells narrowly contiguous (some extralimital spp.); apical abdominal tergum (female) or sternum (male) with horn-like projection; ovipositor strongly projecting. Larva with reduced, lobe-like thoracic legs and 1–3-segmented antennae; abdominal segment 10 with suranal process.

Siricids are native to the Northern Hemisphere with introduced species occurring in Australia, New Zealand and South America (D. R. Smith 1978). Larvae develop in 2–4 years in conifer (SIRICINAE) or angiosperm (Tremecinae) wood. In south-eastern Australia, *Sirex noctilio* is a pest of introduced conifers, especially *Pinus radiata*. Females oviposit into standing or freshly fallen logs, injecting simultaneously mucus and fungal spores. The siricid larvae feed on the mycelia of the wood-rotting fungi. Fire-damaged or drought-stressed trees are particularly susceptible to fatal attack by siricids and their associated fungi (K. L. Taylor 1981).

**3. Orussidae** (Fig. 42.16j). Adult 2.2–13 mm; vertex with rasp-like tubercles (Fig. 42.3b); hypostomal bridge

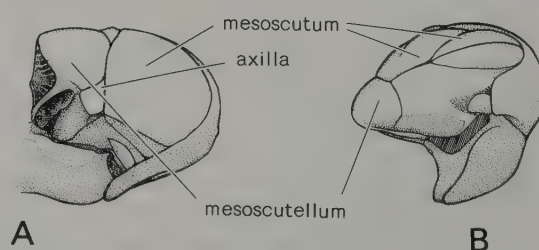


Fig. 42.15 Mesoscutellum and axillae: A, Siricoidea (*Guiglia* sp., Orussidae); B, Tenthredinoidea (*Pterygophorus* sp., Pergidae). [S. Monteith]





Fig. 42.16 Symphyta: A, *Pterygophorus* sp., Pergidae-Pterygophorinae; B, *Philomastix* sp., Pergidae-Philomastiginae; C, *Phylacteophaga froggatti*, Pergidae-Phylacteophaginae; D, *Perga affinis*, Pergidae-Perginae; E, *Clarissa* sp., Pergidae-Euryinae; F, *Pseudoperga* sp., Pergidae-Perginae; G, *Trichorhachus* sp., Argidae; H, *Caliroa cerasi*, Tenthredinidae; I, *Sirex noctilio*, Siricidae; J, *Guiglia sericata*, Orussidae; K, *Austrocyrta australiensis*, Xiphydriidae. [M. Quick]

separates oral cavity from foramen magnum; eyes with minute hairs; antennae inserted low on head, below apparent clypeus, close to oral margin; antennae 11-segmented in males, 10-segmented in females; in females penultimate antennal segment elongate and swollen, apical segment small and peg-like; neck short; fore tibia of female swollen, with a joint-like annular constriction (Figs 42.7D, K); tarsi generally 5-segmented; fore tarsus

of female 3-segmented, with basitarsus apically produced; wing venation often de-pigmented and reduced; hind wing without cross-veins *r-m* and *m-cu*; apical abdominal segment without horn-like projection; ovipositor very long, at rest coiled within abdomen. Larva with thoracic legs reduced to sclerotised discs; antennae 1-segmented; abdominal segment 10 without suranal process; stout and similar to larvae of Apocrita but with transverse rows of

tergal bristles. The hairy eyes, antennae inserted near the mouth, the female fore leg and ovipositor, and the larva are all unique within the Symphyta.

Adult orussids are attracted to sunlit, smooth tree trunks and logs. Their jerky antennal and body movements are remarkably ant-like and the ant-like appearance of some species is accentuated by the patterned fore wings which, at rest, give the impression of a constricted waist. Some species, with swollen hind femora, can jump with great agility. The modified fore leg of females possibly is an acoustic organ which assists in locating oviposition sites. Females oviposit in dry wood into the frass-filled galleries of cerambycid, buprestid or siricid larvae. Eggs are deposited on or near the host larvae and the orussid larvae develop ectoparasitically on these, later entering the host's remains to pupate. A few observations suggest that larvae may also feed on frass or fungus in the host galleries.

Longitudinal carinae are present between the eyes in *Guiglia* (6 spp.) but are absent in the two endemic genera, *Orussobaius* (4 spp.) and the extremely flattened *Orussonia* (1 sp.). [Riek 1955b; D. R. Smith 1988]

### Superfamily TENTHREDINOIDEA

Adult head without subantennal groove; occipital foramen (at least in primitive tenthredinoids) continuous with oral cavity; mesonotum without transverse suture or groove, axillae not defined (Fig. 42.15B). Larva usually with well-developed thoracic legs and abdominal prolegs; stemmata present; abdominal segment 10 sometimes with median process but this fleshy.

Females insert their eggs in plant tissue and larvae feed on leaves or stems, mostly of angiosperms. Some extralimital tenthredinids are gall-dwelling. Pupation takes place either in the ground or, in the case of concealed feeders, in the larval tunnel, mine or gall.

Blasticotomidae (a primitive, Palaearctic family with larvae boring in fern stems), Cimbicidae (adult abdomen laterally with sharp, longitudinal fold; larvae feeding externally on woody angiosperms) and Diprionidae (predominantly Holarctic; larvae feeding on conifer needles) are absent from Australia. The venation of the anal area of Pergidae is reduced compared to that of other tenthredinoids and most other Symphyta.

**4. Tenthredinidae** (Fig. 42.16H). Adult 3.5–7 mm (Australian species); antennae 7–23-segmented; oral cavity and foramen magnum continuous; neck short; fore wing usually with cross-vein 2r (absent in some extralimital species); fore tibia with 2 apical spurs, one usually apically cleft (simple in some extralimital species). Larva usually with 5-segmented thoracic legs (with claws), and abdominal prolegs on segments 2–7 or 8 and 10 (legs reduced in leaf-miners); stemmata present; antennae variable, from disc-like to 5-segmented.

This is the largest symphytan family with 5000 species world-wide, predominantly in the Northern Hemisphere. In Australia the family is represented by the endemic genus *Cheilophleps* (1 sp.), a species of *Senoclidea* which also occurs in New Guinea, and two introduced species.

*Caliroa cerasi* is an almost cosmopolitan pest, its slug-like, exudate-covered larvae skeletonising leaves of cherry, plum and pear trees. *Priophorus morio*, introduced from the Holarctic region, attacks raspberry, blackberry and loganberry bushes. [Benson 1938a]

**5. Argidae** (Fig. 42.16G). Adult 3.8–12 mm; antennae 3-segmented, apical segment elongate and sometimes bifid; oral cavity and foramen magnum continuous; neck short; fore wing without cross-vein 2r; fore tibia with 2 unmodified, apical spurs. Larva with 5-segmented thoracic legs with or without claws, and abdominal prolegs on segments 2–7 or 8 and 10; stemmata present; antennae 1–4-segmented.

This cosmopolitan family with about 800 species world-wide is poorly represented in Australia. Females of some extralimital genera stand guard over gregarious, young larvae.

#### Key to the Subfamilies of Argidae Known in Australia

1. Anal cell of fore wing with oblique cross-vein ..... ZENARGINAE  
     Anal cell of fore wing petiolate (Fig. 42.16G) or constricted medially ..... 2
- 2(1). Antennae bifid in ♂ ..... STERICTIPHORINAE  
     Antennae simple ..... ARGINAE

*Zenarge turneri*, the sole species of ZENARGINAE, occurs only in south-eastern Australia where larvae feed on *Callitris* and introduced *Cupressus*.

STERICTIPHORINAE are most diverse in the Neotropical region. Larvae of *Schizocerella pilicornis*, a species introduced from the New World, are leaf-miners in *Portulaca*. *Trichorhachus* (4 spp.) are endemic to south-western W.A., where larvae feed on smoke bush (*Conospermum*).

Larvae and host plants are not known for the endemic genus *Antargidium* (6 spp.), the only representative of the cosmopolitan ARGINAE. [Benson 1963]

**6. Pergidae** (Figs 42.16A–F). Adult 2.8–30 mm; antennae 5–24-segmented; head sometimes with complete hypostomal bridge; neck short; fore wing without cross-vein 2r; fore tibia with 1 or 2 apical spurs. Larva (Figs 42.13A–D) with 3–5-segmented legs with claws; abdominal prolegs on segments 2–6, 2–8 or 3–8 and 10, sometimes only on 10 or completely absent; stemmata present; antennae variable from disc-like to multisegmented.

Pergids are the most common Australian sawflies. The family is diverse in Australia and South America with a few species in the Nearctic and Oriental regions and in New Guinea. Syzygoniinae, Acordulecerinae, Loboceratinae, Paralyphiinae and Conocoxinae are restricted to Central and South America. Perreyiinae, with several genera in the New World, are represented in Sulawesi and New Guinea by *Cladomacra*, some females of which are apterous (Naumann 1984).

Females of Philomastiginae and some Perginae stand guard over eggs and young larvae, and buzz their wings and stridulate when disturbed.



## Key to the Subfamilies of Pergidae Known in Australia

1. Fore wing with closed, petiolate anal cell (Fig. 42.16E; cell open apically in *Ancyloneura*) ..... 2  
Fore wing without petiolate anal cell (Figs 42.16A–D, F) ..... 3
- 2(1). Tibiae without preapical spurs (Fig. 42.16E); all radial cells of fore wing distinct; propodeum uniformly, strongly sclerotised ..... EURYINAE  
Mid and hind tibiae each with preapical spur; 1st and 2nd radial cells fused; propodeum strongly emarginate posteriorly, with only the anterior margin and sides strongly sclerotised ..... STYRACOTECHYINAE
- 3(1). Mesoscutellum not lobed or produced posterolaterally, at most slightly emarginate posteromedially ..... 4  
Mesoscutellum lobed or produced posterolaterally .. 7
- 4(3). First *cu-a* cross-vein of fore wing very oblique (Fig. 42.16c) ..... PHYLACTEOPHAGINAE  
First *cu-a* cross-vein of fore wing transverse or almost so (Fig. 42.16A) ..... 5
- 5(4). 1st and 2nd radial cells of fore wing fused; fore tibia with 1 spur ..... PERGULINAE  
2nd and 3rd radial cells of fore wing joined (Fig. 42.16A); fore tibia with 2 spurs ..... 6
- 6(5). Tibiae without preapical spurs ..... PTERYGOPHORINAE  
Mid and hind tibiae each with preapical spur ..... PTERYPERGINAE
- 7(3). First *cu-a* cross-vein of fore wing arising close to junction between M and CuA (Fig. 42.16D); all radial cells of fore wing well developed .. PERGINAE  
First *cu-a* cross-vein of fore wing arising from the middle of the 1st median cell (Fig. 42.16B); 1st radial cell of fore wing very small ..... PHILOMASTIGINAE

PERGINAE (58 spp.; Figs 42.13B, 16D) include the largest species and their larvae, which lack abdominal prolegs, are often conspicuous defoliators of *Eucalyptus* and *Angophora*. Larvae store *Eucalyptus* oils in a fore gut diverticulum and regurgitate these when attacked. Females insert their eggs in batches in leaves and induce small swellings. *Perga* (19 spp.) are sometimes pests in south-eastern Australia. Their larvae disperse over trees to feed at night, aggregate on branches or trunks by day, and pupate in soil and litter. Adults emerge over two seasons. The subfamily is restricted to Australia and New Guinea.

PHYLACTEOPHAGINAE (5 spp.; Figs 42.13D, 16C) are endemic to eastern and south-western Australia but one species of *Phylacteophaga* has been introduced accidentally to New Caledonia and New Zealand. Larvae of *Phylacteophaga* (3 spp.) are flattened, lack abdominal prolegs and cause blotch mines on leaves of *Eucalyptus* and *Tristania*. Larvae pupate inside the mines. [Naumann 1983]

Adults of PTERYGOPHORINAE (17 spp.; Fig. 42.16A) are often attractively banded in orange or yellow, with partially darkened wings, and the antennae of some males are spectacularly comb-like. Larvae have a median, dorsal process on abdominal segment 10, and feed on *Calli-*

*stemon*, *Melaleuca*, *Leptospermum*, *Emex* and *Rumex*. *Lophyrotoma interrupta* larvae feed on *Eucalyptus* and *Angophora* and are sometimes eaten by cattle which they poison. The subfamily is restricted to Australia and New Guinea.

EURYINAE (54 spp.; Fig. 42.16E) are generally small (5–7 mm). Adults are sometimes common on flowers and the mouth-parts of *Euryis* (10 spp.) are elongate to reach deep nectaries. Males of *Polyclonus* (1 sp.) have feather-like antennae. Euryine larvae, which have a pair of dorsal pronotal lobes, are found in leaf litter or sheltering under bark and in at least some species feed on dead or dying leaves. Larvae of *Warra* (2 spp.) develop on the semi-aquatic fern *Marsilea*. The subfamily is restricted largely to Australia (6 endemic genera); *Ancyloneura* occurs in New Guinea.

PHILOMASTIGINAE (2 spp.; Figs 42.13A, 16B) occur in Australia and South America. Larvae of *Philomastix* (2 spp.) have a pair of dorsal processes on abdominal segment 9 and shorter, paired processes on abdominal segment 10, and feed on *Rubus* spp.

PERGULINAE occur only in south-western Australia (*Pergula*; 1 sp.) and South America. PTERYPERGINAE (*Pteryperga*, 2 spp.; larvae on *Elaeocarpus*) and STYRACOTECHYINAE (*Styracotechys*; 1 sp.) are endemic. [D. R. Smith 1978]

## Suborder APOCRITA

Adults with segment 1 of abdomen (propodeum) fused to thorax (e.g. Fig. 42.1B). Usually there is a constriction (waist) between the propodeum and the metasoma or gaster (absent in some Mymaridae, Aphelinidae, Signiphoridae and Trichogrammatidae). Larvae apodous, head capsule usually somewhat reduced (Figs 42.13E–J).

The suborder is divided into two large groups—the terebrant or ‘parasitic’ superfamilies and the ‘aculeate’ superfamilies.

Larvae of terebrant Hymenoptera (Stephanoidea, Trigonalioidea, Megalyroidea, Ceraphronoidea, Evanioidea, Ichneumonoidea, Cynipoidea, Proctotrupoidea, Platygasteroidea, Chalcidoidea) develop as parasites of other arthropods or as phytophages in plant galls. The terebrants include the most morphologically primitive Apocrita (Stephanoidea, Trigonalioidea, Megalyroidea) and presumably evolved from some orussid- or cephid-like symphytan during the late Triassic or early Jurassic.

The prepectus is exposed in most Symphyta but concealed in all Siricoidea (except Anaxyelidae) and Apocrita. Possibly concealment of the prepectus is a synapomorphy for the Siricoidea (excluding Anaxyelidae) + Apocrita. Orussidae and Apocrita probably are sister groups, the synapomorphies being the linear parapsidal lines, the loss of the postspiracular sclerite, rigid abutment of the metanotum and T1 (without an exposed metapostnotum), and the presence of a pronotal lobe. This would suggest that the parasitic way of life so typical of Apocrita had its origin in an orussid-like life cycle in which the female oviposited into galleries in wood and her larvae located and fed on larvae of other insects in the galleries. None of the extant, primitive Apocrita exhibit

such a life cycle but both Stephanoidea and Megalyroidea do parasitise larvae in wood. Megalyrids have a subocular groove similar to that of siricoids but have a somewhat specialised prepectal morphology.

The somewhat narrowed waist of Cephoidea recalls the typical wasp waist of Apocrita and has led some authors to suggest that these stem-borers are ancestral to the Apocrita.

The trigonalid life cycle is simple in that the female lays numerous eggs on foliage and these are ingested by phytophagous larvae. This strategy is possibly a primitive one but it is unlikely that trigonalids gave rise to the remainder of the terebrants. Trigonalid larvae are specialised in that they mostly develop as hyperparasites on other parasites within the body of the phytophagous host.

Irrespective of how parasitism arose, the next stage in its evolution saw the female locating and ovipositing on or into the host and increased sophistication of structures associated with host location and egg laying.

The phylogeny of the terebrant families is controversial (Königsmann 1978a,b; Rasnitsyn 1988; Gibson 1985, 1986a). The Evanioidea and Proctotrupeoidea possibly are not monophyletic and the relationships among the superfamilies are disputed. A number of similar morphological changes appear to have taken place independently in unrelated taxa and these confound attempts to reconstruct a phylogeny. These changes include reduction in size, in wing venation, in the number of metasomal spiracles and in the number of antennal segments, loss of mobility of the pronotum, incorporation of the mesothoracic spiracle in the pronotum, exposure of the prepectus or its fusion with adjacent sclerites, loss of the median mesoscutal sulcus and concealment of the ovipositor.

The aculeate Hymenoptera (Chrysoidea, Vespoidea, Sphecoidea, Apoidea) are a monophyletic assemblage defined by a feature of the ovipositor (the 2nd valvifer is divided into 2 parts by a dorsoventral constriction) and by the loss of the cerci from females (Brothers 1975).

In Chrysoidea the 2nd valvifer is completely divided and the two parts articulate, a character state unique with-

in the aculeates. This superfamily probably is the sister group to the remaining aculeates. Most chrysidoids are parasitic but some Bethyidae are incipient predators in that females drag host larvae which they have stung to pre-existing places of concealment. One Nearctic bethylid is known to construct a small nest in the nests of other fossorial wasps, and its behaviour thus parallels that of some primitive Pompilidae and Sphecidae.

T8 of the female is retracted and medially desclerotised in all aculeates except Chrysoidea, which suggests that the Sphecoidea + Apoidea + Vespoidea is a monophyletic unit. In almost all non-chrysidoid aculeates the antennae are 12-segmented in females and 13-segmented in males.

Apoidea and Sphecoidea are closely related and almost certainly form a monophyletic group (Lomholdt 1982), and a sister group to the Vespoidea. In Apoidea and Sphecoidea, but not in Vespoidea, the pronotum is reduced posteriorly above the level of the tegula but forms a distinct lobe below the level of the tegula, covering the spiracle. In apoids and sphecoids the metapostnotum is enlarged and forms the anteromedial 'propodeal triangle'. Females of the most behaviourally primitive Sphecoidea sting and oviposit on large prey in their own retreats and construct no nest. Behaviourally more advanced sphecids excavate or construct complex nests and provision these with generally smaller prey. Apoidea have abandoned entomophagous habits and provision their larval cells with pollen and nectar or floral oils. Social behaviour has evolved independently within both the Sphecoidea and Apoidea.

The metapostnotum is reduced in the Vespoidea but generally the vespoid families are not associated by any particularly strong character state. Once again, the more primitive families in the assemblage are entirely parasitic and predatory behaviour has evolved independently in several families (Pompilidae, Vespidae and Formicidae). Masarine vespids have become secondarily bee-like in provisioning their cells with pollen and nectar. Social behaviour has also evolved independently in Vespidae and Formicidae.

#### *Key to the Superfamilies of Apocrita as Represented in Australia*

1. Hind tibia with 1 or 2 spurs (if spurs absent then antennae with more than 13 segments) but none modified into calcar ..... 2  
 When hind tibial spur or spurs present, one or both modified into a calcar through development of a comb of hairs or teeth (Figs 42.7s-v); corresponding comb or brush developed on slightly emarginate hind basitarsus (Fig. 42.7c); if spurs absent then antennae with fewer than 13 segments ..... 24
- 2(1). Head with crown of teeth; petiole longer than wide; fore wing well developed, with numerous closed cells (Fig. 47.17c) ..... STEPHANOIDEA (p. 938)  
 Without the above combination of character states ..... 3
- 3(2). Subantennal groove present (Fig. 42.3a); hind tibia with apical cleaning brush ..... MEGALYROIDEA (p. 939)  
 Subantennal groove absent; hind tibia without apical cleaning brush ..... 4
- 4(3). Metasoma attached to propodeum well above hind coxae (Fig. 42.1b); fore wing well developed with numerous closed cells, including costal cell ..... EVANIOIDEA (p. 941)  
 Without the above combination of character states ..... 5
- 5(4). Wings well developed, at rest extending well beyond mid point of metasoma ..... 6  
 Wings reduced (not extending beyond mid point of metasoma) or absent ..... 16
- 6(5). Posterolateral corner of pronotum not reaching tegula (Fig. 42.5c) ..... 7  
 Posterolateral corner of pronotum reaching tegula (Fig. 42.5d) ..... 8
- 7(6). Fore wing with closed basal cells (Figs 42.29H, K) ..... CHRYSIDOIDEA (pt, p. 970)



- Fore wing without closed basal cells (Figs 42.25–28) ..... CHALCIDOIDEA (pt, p. 955)
- 8(6). Spiracle cover lobe of pronotum margined with close, fine hairs ..... 9  
Spiracle cover lobe of pronotum not margined with close, fine hairs ..... 10
- 9(8). Pronotum with well-developed dorsal surface, posterodorsal margin at most weakly concave .....  
..... VESPOIDEA (pt, p. 974)  
Pronotum without well-developed dorsal surface, posterodorsal margin strongly concave .....  
..... TRIGONALYOIDEA (p. 938)
- 10(8). Costal cell absent (Figs 42.19, 20); pterostigma present; fore wing with at least one closed basal cell .....  
..... ICHNEUMONOIDEA (pt, p. 943)  
Without the above combination of character states ..... 11
- 11(10). Lateral panel of pronotum flat, or slightly convex, not vertically grooved for reception of fore femur; antennal sockets  
closer to each other than to eye ..... CYNIPOIDEA (p. 954)  
Without the above combination of character states ..... 12
- 12(11). Either hind femur enlarged, toothed (Fig. 42.25G); or antennal sockets widely separated, closer to eyes than to each  
other; or body metallic ..... CHALCIDOIDEA (pt, p. 956)  
Hind femur not enlarged and toothed; antennal sockets closer to each other than to eyes; body not metallic ..... 13
- 13(12). Fore tibia with 2 apical spurs; closed costal cell absent (Fig. 42.17D); radial vein long and without apical knob; median  
mesoscutal sulcus often present [metasoma with distinct anterior face, defined posteriorly by dorsal and ventral  
transverse carinae] ..... CERAPHRONOIDEA (pt, p. 940)  
Fore tibia with 1 apical spur; if closed costal cell absent then radial vein short and with apical knob (Fig. 42.23i) or  
venation absent (Fig. 42.23k) or head, antennae and legs with conspicuous flanges (Fig. 42.29i); median mesoscutal  
sulcus absent ..... 14
- 14(13). Antennae inserted well above frontoclypeal suture (Figs 42.2, 22); if inserted on a frontal protuberance then T2 and  
S2 fused without trace to form cylinder (Fig. 42.22) ..... PROCTOTRUPOIDEA (pt, p. 949)  
Antennae inserted very close to frontoclypeal suture (separated from suture by at most the diameter of the antennal  
socket, Fig. 42.23); antennae rarely inserted on frontal protuberance but if so then T2 and S2 not fused to form  
cylinder (Fig. 42.29E) ..... 15
- 15(14). Fore wing without closed, basal cells (Fig. 42.23) ..... PLATYGASTEROIDEA (pt, p. 952)  
Fore wing with at least one closed, basal cell (Figs 42.29A, B, D–F, I) ..... CHRYSIDOIDEA (pt, p. 970)
- 16(5). Antennae with 16 or more segments ..... ICHNEUMONOIDEA (pt, p. 943)  
Antennae with 15 or fewer segments ..... 17
- 17(16). Antennae inserted on distinct frontal protuberance (as in Fig. 42.22H); T2 and S2 fused to form cylinder .....  
..... PROCTOTRUPOIDEA (pt, p. 949)  
Without the above combination of character states ..... 18
- 18(17). Fore tibia with 2 apical spurs ..... CERAPHRONOIDEA (pt, p. 940)  
Fore tibia with 1 apical spur ..... 19
- 19(18). Either tarsi 3- or 4-segmented; or antennal sockets closer to eyes than to each other; or mid basitarsus enlarged, with  
stout ventral setae (Fig. 42.7w); or cerci advanced (Fig. 42.27H) ..... CHALCIDOIDEA (pt, p. 956)  
None of the above ..... 20
- 20(19). Metasoma with at most one pair of spiracles ..... 21  
Metasoma with more than one pair of spiracles ..... 22
- 21(20). Metasoma with one pair of spiracles ..... CHALCIDOIDEA (pt, p. 956)  
Metasoma without spiracles ..... PLATYGASTEROIDEA (pt, p. 952)
- 22(20). Either tegula present (Fig. 42.29j); or antennae inserted on frontal protuberance (as in Fig. 42.29E); or fore tarsus  
chelate (Fig. 42.29c) ..... CHRYSIDOIDEA (pt, p. 970)  
None of the above ..... 23
- 23(22). Mandibles large, often sickle-shaped; hind tibia with spine-like setae; metasomal terga often with transverse carinae  
..... VESPOIDEA (pt, p. 974)  
Mandibles not large, not sickle-shaped; hind tibia usually without spine-like setae; metasomal terga without transverse  
carinae ..... CHRYSIDOIDEA (pt, p. 970)
- 24(1). 1st (and sometimes also 2nd) metasomal segment node-like (i.e. strongly constricted anteriorly and posteriorly,  
enlarged medially, Figs 42.34, 36, 40); felt lines absent; posterolateral corner of mesosoma usually with opening of  
metapleural gland (Fig. 42.35); apterous worker caste present ..... VESPOIDEA (pt, p. 974)  
If 1st metasomal segment node-like then felt lines (Figs 42.32A, B) present; without apterous worker caste; opening of  
metapleural gland absent ..... 25
- 25(24). Body with at least a few plumose or branched hairs (Fig. 42.44D); never apterous; hind basitarsus often thicker than  
following segments (Fig. 42.45) ..... APOIDEA (p. 993)  
Body usually without plumose or branched hairs (such hairs present only in some apterous forms); wings variable in  
length or absent; hind basitarsus not thicker than following segments ..... 26
- 26(25). Mesosoma dorsally without transverse sutures (Fig. 42.32B); apterous; felt lines present ..... VESPOIDEA (pt, p. 974)  
Mesosoma dorsally with at least some transverse sutures; wings variable in length or absent; felt lines absent ..... 27
- 27(26). Pronotum extending posteriorly above tegula as acute process (Fig. 42.33); fore wing often longitudinally folded  
when at rest ..... VESPOIDEA (pt, p. 974)

- Pronotum not extending posteriorly above tegula as acute process (Figs 42.30, 32, 41); fore wing not longitudinally folded when at rest ..... 28
- 28(27). Lateral panel of pronotum ventrally rounded (Fig. 42.30) ..... VESPOIDEA (pt, p. 974)
- Lateral panel of pronotum ventrally acute (e.g. Figs 42.32j, 41) ..... 29
- 29(28). Pronotum with rounded, posterolateral spiracle cover lobe (Fig. 42.41); mid coxae not covered by mesosternal lobes ..... SPHECOIDEA (p. 989)
- Pronotum without rounded spiracle cover lobe; mid coxae basally partially covered by mesosternal lobes (Fig. 42.32k) ..... VESPOIDEA (pt, p. 974)

### Superfamily STEPHANOIDEA

Antennae multisegmented, filiform; subantennal groove weak. Pronotum mobile on mesothorax and extending posteriorly to tegula, concealing spiracle. Prepectus present, discrete, concealed beneath posterolateral edge of pronotum. Mesoscutum usually with median sulcus. Axillae large, contiguous. Fore wing with pterostigma; costal cell present. Hind wing venation reduced. Trochantellus present. Hind tibia and tarsi with cleaning brushes of dense setae. Petiole moderately to very long; formed by T2 and S2, these sometimes fused to form a cylinder. Cerci digitiform. Larvae with transverse rows of small spines; mandibles broad basally, tapering to a 3-toothed apex.

The Stephanioidea do not appear to be closely related to any other extant Apocrita. In the development and position of the prepectus and mesothoracic spiracle stephanoids resemble Orussidae, and preserve the most primitive condition of these structures known in the Apocrita. Stephanoids retain several other morphological features apparently plesiomorphic for the Apocrita (mobile pronotum, median mesoscutal sulcus, large and contiguous axillae) and probably represent a very ancient lineage (Gibson 1985; Rasnitsyn 1988).

**7. Stephanidae** (Fig. 42.17c). Adults are slender (3.5–60.0 mm), long necked, mostly dark bodied and sometimes with darkened wings, and superficially resemble some Gasteruptiidae or Doryctinae (Braconidae). The exerted ovipositor is up to 2 times as long as the rest of the body. The mobile, globular head bears rasp-like teeth, similar to those on the vertex and frons of Orussidae. The mid tibia lacks spurs. On the hind leg the femur is usually toothed, the tibia distally swollen, and in many females the number of tarsal segments reduced to 4 or 3.

The family is cosmopolitan but most diverse in tropical regions (E. A. Elliott 1922). Stephanids parasitise wood-boring larvae and native Australian species have been reared from bostrichid-infested hardwoods (Rodd 1951; K. M. Moore 1961a). *Schlettererius cinctipes* was introduced from North America for the biocontrol of *Sirex noctilio* (K. L. Taylor 1981). Adult stephanids are found on tree trunks, limbs and logs, and females oviposit through apparently sound wood. A few species are attracted to light.

### Superfamily TRIGONALYOIDEA

Antennae multisegmented, filiform, their bases each concealed by frontal lamella (this sometimes weak); subantennal groove absent. Pronotum somewhat mobile on mesothorax, posteriorly reaching tegula; pronotal lobe concealing spiracle (except in the extralimital *Nomadina*). Prepectus fused to pronotum, posterior pronotal inflection

present. Mesoscutum without median sulcus. Axillae small, widely separated. Fore wing venation very complete; costal cell and pterostigma present. Cell 1Rs usually distinctively shaped, sometimes fused with 2Rs. Hind wing with 2 closed cells. Mid and hind legs each with trochantellus. Hind tibia and tarsi without conspicuous cleaning brushes. Tarsi with plantar lobes. S7 of female apically channeled, pointed, stiffened. Cerci digitiform. First instar larva microtype, 3rd instar mandibulate; mature larva with 3-toothed mandible. Cocoon present or absent.

Trigonalalyoids preserve possibly the most complete and primitive wing venation in the Apocrita (Figs 42.8c, d). They appear to be an archaic terebrant group and not closely related to primitive aculeates as sometimes suggested (see Königsmann 1978a; Rasnitsyn 1988). However, by virtue of their distinctive wing venation, frontal lamellae and apically down-curved metasoma, trigonalalyoids occupy an isolated position among the parasitic families.

**8. Trigonalalyidae** (Fig. 42.17b). This small family is cosmopolitan with about 100 spp. world-wide. Medium sized (3.5–13 mm) and stout-bodied, adults superficially resemble some Sphecoidea or Apoidea. The mandibles are broad with stout teeth. The number of antennal segments is sometimes variable within a species.

To oviposit the female trigonalalyid stands on the upper surface of a leaf, curls her metasoma beneath the leaf, and inserts her eggs in small, submarginal incisions. Several eggs may be deposited per leaf. Females can lay several thousand very small (0.7–0.15 mm) eggs. The eggs are eaten accidentally by phytophagous larvae of Lepidoptera or Symphyta and hatch in their alimentary canal. Within a few hours the 1st instar trigonalalyid larva pierces the wall of the alimentary canal and enters the body cavity of the phytophagous larva. Possibly some trigonalalyids develop as primary parasites of phytophagous larvae and emerge from the host cocoons but most evidence indicates that they are secondary parasites (i.e. hyperparasitic)—if the primary, phytophagous larva is parasitised by an endoparasitic ichneumonid or tachinid, the trigonalalyid larva enters the body of the ichneumonid or tachinid larva and emerges ultimately from the cocoon or puparium of the primary parasite. A Nearctic trigonalalyid is hyperparasitic on a tachinid parasite of a tipulid larva which feeds on decaying plant material. Some extralimital trigonalalyids have been reared from the cells of Vespinae and Polistinae (Vespidae). Adults of these vespids feed their larvae the body fluids and shreds of other insects, including lepidopterous larvae. Presumably it is in this way that trigonalalyid larvae, formerly within lepidopterous larvae, are introduced inadvertently to the vespid larvae.



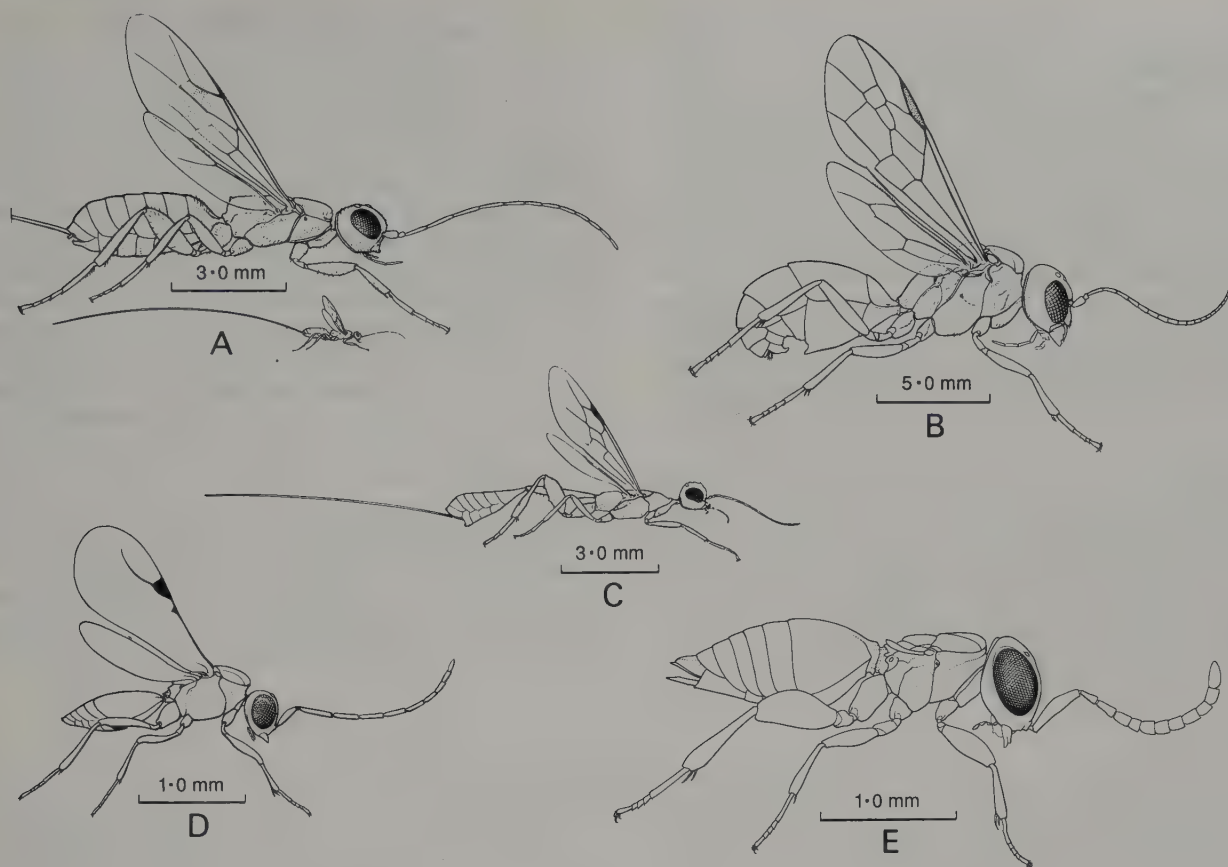


Fig. 42.17 A, *Megalyra* sp., Megalyridae; B, *Taeniogonalos* sp., Trigonalyidae; C, unidentified Stephanidae; D, E, *Conostigmus* sp., Megaspilidae ♂, ♀. [A–C by M. Quick; D by S. Monteith; E by T. Nolan]

Hosts may be infested initially with more than one trigonalysid larva but only one trigonalysid emerges ultimately from each host. Trigonalyid larvae are initially endoparasitic but the last instar feeds externally (Yamane 1973). Trigonalyids pupate within the host cocoon or cell. Adults are short lived; in Australia they are seen occasionally in summer and autumn on eucalypt foliage.

In Australia *Taeniogonalos* (7 spp.) has been reared both as a hyperparasite [from Perginae (Pergidae) and *Anthela* (Anthelidae) in which a tachinid or ichneumonid was a primary parasite] and as a primary parasite (from *Perga*, Geometridae and Tortricidae). During oviposition the median process on S3 (and sometimes S4) of female *Taeniogonalos* grips the upper surface of the leaf more or less directly above the point where the egg is being deposited. Female *Mimelogonalos* (6 spp.) lack these processes. *Taeniogonalos* extends into Melanesia and *Mimelogonalos* is endemic. [Clausen 1940; Riek 1954f, 1962a, 1962b]

#### Superfamily MEGALYROIDEA

Antennae 14-segmented, usually filiform (clavate in the Oriental *Carminator*); subantennal groove present. Prepectus absent. Posterior pronotal inflection absent. Mesoscutum usually with median sulcus (this obscured in some coarsely sculptured species). Axillae usually large,

contiguous or narrowly separated. Fore wing with pterostigma reduced or absent; costal cell present. Hind wing venation reduced. Trochantellus present. Hind tibia and basitarsus each with medial, cleaning brushes of dense setae. Metasoma anteriorly broad but with a very short petiole formed by anterior extensions of T2 and S2. Cerci digitiform.

Possibly the Megalyroidea are most closely related to the Ceraphronoidea (Gibson 1985; Rasnitsyn 1988). They are the only Apocrita in which the mesothoracic spiracle is entirely surrounded by pronotal cuticle and which also lack a posterior pronotal inflection. An enclosed spiracle also occurs in Proctotrupidae and Pelecinidae. The condition seems to have arisen similarly in the Megalyroidea and Ceraphronoidea, but via different transformations in the Proctotrupidae and Pelecinidae, both of which have a posterior pronotal inflection. Other characteristic features of the Megalyroidea possibly are plesiomorphic for the Apocrita as a whole: a subantennal groove is present also in Stephanoidea (although weakly defined) and some Symphyta (Orussidae, Xiphydriidae, Siricidae); a hind tibial cleaning brush occurs in the Orussidae; and the median sulcus of the mesoscutum is present in many Ceraphronoidea and Symphyta and in some Stephanidae, and probably is plesiomorphic for the Hymenoptera as a whole (Gibson 1985; S. R. Shaw 1988). The megalysid

metasoma lacks the transverse, anterior carinae present in Ceraphronoidea.

**9. Megalyridae** (Fig. 42.17A). These small to very large (2.5–100 mm) wasps are mostly dark bodied, usually with banded or uniformly darkened fore wings. The exerted ovipositor is up to 8 times as long as the rest of the body. The family occurs in Australia, the Oriental and Melanesian regions, Africa, Madagascar and South America, but is most diverse in Australia where there are numerous species of *Megalyra*. Only the MEGALYRINAE are represented in Australia. Dinapsinae, all of which have a distinct, postocular carina, are restricted to South America, Africa, Madagascar and the Oriental region.

Most species of *Megalyra* appear to parasitise the immature stages of wood-boring Coleoptera (Rodd 1951; Naumann 1987b). Wasps are sometimes seen walking on tree trunks or limbs. Once a host tunnel is located oviposition takes place through either the frass plug or sound wood. *Megalyra troglodytes* is endoparasitic in the immature stages of an *Arpactophilus* (Pemphredoninae: Sphecidae) which reoccupies abandoned nests of mud-dauber wasps. Males of *Megalyra mutilis* are micropterous.

## Superfamily CERAPHRONOIDEA

Parasitic or hyperparasitic. Ceraphronoids are distinguished from all other Apocrita (except *Nothomyrmecia*, Formicidae) by having 2 apical spurs on the fore tibia. Antennae 7–11-segmented in females; 11-segmented in males; scape relatively long (length more than 2.5 times width); subantennal groove absent. Prepectus absent; posterior pronotal inflection absent. Mesoscutum often with median sulcus. Fore wing with or without pterostigma, costal cell absent, radial cell open; radial vein usually long, curved or straight, rarely absent. Hind wing venation very reduced. Trochantellus sometimes present. T2 and S2 separated by suture; metasoma with distinct anterior face, defined posteriorly by dorsal and ventral, transverse carinae; ovipositor concealed within metasoma at rest. First instar larva hymenopteriform. Mature larvae with tubercles or sclerotised rings.

Ceraphronoids are often very common in leaf litter. There are many forms with reduced wings and these sometimes have a conspicuously enlarged pronotum. Most Australian species belong to cosmopolitan genera. [Dessart and Cancemi 1986]

### Key to the Families of Ceraphronoidea

1. Fore wings large, at rest extending beyond posterior tip of metasoma ..... 2
- Fore wings reduced or absent, not extending beyond posterior tip of metasoma ..... 5
- 2(1). Fore wings with large pterostigma (Fig. 42.17D) ..... **Megaspilidae** (pt, p. 940)
- Fore wings without pterostigma ..... 3
- 3(2). ♀♀; antennae 10-segmented ..... **Ceraphronidae** (pt, p. 940)
- ♂♂; antennae 11-segmented ..... 4
- 4(3). Metasoma anterodorsally with 3 longitudinal carinae ..... **Megaspilidae** (pt, p. 940)
- Metasoma anterodorsally with numerous longitudinal carinae, although these sometimes short ..... **Ceraphronidae** (pt, p. 940)
- 5(1). Pronotum mid-dorsally longer than mesoscutum, or sutures of mesosoma almost completely absent ..... **Megaspilidae** (pt, p. 940)
- Pronotum mid-dorsally shorter than mesoscutum; mesosoma always with numerous sutures ..... 6
- 6(5). Antennae of ♀♀ with 10 or fewer segments; mesoscutum with or without median sulcus, notauli absent ..... **Ceraphronidae** (pt, p. 940)
- Antennae of ♀♀ with 11 segments; mesoscutum usually with median sulcus and notauli ..... **Megaspilidae** (pt, p. 940)

**10. Ceraphronidae.** Minute to small (0.5–2.1 mm); antennae of females 7–10-segmented; mesoscutum sometimes with median sulcus, notauli absent; in wing-reduced forms the mesosoma tends to be only slightly modified compared with that of fully winged forms; longer fore tibial spur not apically forked; mid tibia with 1 spur; pterostigma absent; petiole and anterior face of gaster each formed in part by T2 and S2. Waterston's organ, which presumably is glandular, is always present and sometimes visible through T5 or T6. Cerci plate-like.

*Aphanogmus*, in which the mesosoma is laterally compressed, is mostly hyperparasitic via braconids in larvae of Lepidoptera. The mesosoma is more dorsoventrally depressed in *Ceraphron*, extralimital species of which have been reared as parasites or hyperparasites from various Diptera, parasitic Hymenoptera, Hemiptera and Neuroptera. All ceraphronids are endoparasitic. [Dessart and Cancemi 1986]

**11. Megaspilidae** (Figs 42.17D, E). Minute to small (0.5–3.0 mm); antennae of females 11-segmented; mesoscutum usually with median sulcus and notauli present at least anteriorly; in some wing-reduced forms mesosomatic sulci and sutures are greatly reduced or absent; longer fore tibial spur apically forked; mid tibia with 2 spurs; petiole and anterior face of metasoma formed entirely by T2, the corresponding sternum visible from below as a transverse, horizontal sclerite; Waterston's organ absent; cerci digitiform.

The pterostigma is enlarged in fully winged MEGASPILINAE and T3 usually has numerous basal carinae. *Conostigmus* has been reared from Tachinidae, Syrphidae and Agromyzidae (DIPT) and *Dendrocerus*, in which the basal flagellar segments of some males have long rami, is hyperparasitic via Aphidiinae (Braconidae) in aphids. In LAGYNODINAE the pterostigma is absent in winged males (some males and all females are wingless) and T3 has only



3 basal carinae. Most megaspilids are endoparasitic. [Fergusson 1980; Dessart and Cancemi 1986]

### Superfamily EVANIOIDEA

Antennae 13–14 segmented, filiform. Subantennal groove absent. Prepectus absent. Pronotum not freely mobile on mesothorax, reaching tegula, with spiracle visible at posterior margin or covered by posterior lobe of pronotum. Mesoscutum without median sulcus. Fore wing with pterostigma; costal cell present. Hind wing with costa only, without closed cells. Hind tibia and tarsi without cleaning brushes of dense setae. Metasoma inserted high on propodeum. Cerci present or absent.

The evanioid families have been grouped together prin-

cipally because they share a high insertion of the metasoma on the propodeum. However this character state also occurs in some Ichneumonoidea, Cynipoidea and Chalcidoidea.

Gasteruptiidae and Aulacidae have similar, rigid abutment of the pronotum and the mesepisternum, and similar fusion or partial fusion of T2 and T3. These two families appear to be sister groups, with the Aulacidae retaining the greater number of plesiomorphic features (e.g. more complete fore wing venation). The pronotal-mesepisternal morphology and the metasoma are quite different in the Evaniidae which may not be related closely to the other two families. [Crosskey 1951; Königsman 1978a; Gibson 1985]

#### Key to the Families of Evanioidea

1. T2 and S2 fused to form a cylindrical petiole; 3rd–9th abdominal segments strongly laterally compressed so that metasoma hatchet-shaped (Fig. 42.18A); hind wing with jugal lobe ..... **Evaniidae** (p. 941)
- T2 and S2 not fused to each other, not forming a cylindrical petiole; 3rd–9th abdominal segments weakly laterally compressed, metasoma elongate; hind wing without jugal lobe ..... 2
- 2(1). Metasoma separated from metanotum by less than the anterior width of T2 (Figs 42.18B–D); inner surface of hind coxa of ♀ neither grooved nor notched ..... **Gasteruptiidae** (p. 942)
- Metasoma separated from metanotum by more than the anterior width of T2 (Fig. 42.18E); inner surface of hind coxa of ♀ with groove or notch ..... **Aulacidae** (p. 941)

**12. Evaniidae** (Fig. 42.18A). Stout bodied (2.3–13 mm). Antennae 13-segmented in both sexes. Mouth-parts not elongate. Pronotum reaching posteriorly to tegula, with or without distinct pronotal lobe; prepectus fused internally to pronotum, posterior pronotal inflection present. Metasternum with a posteriorly-directed, bilobed process between hind coxae. Fore wing not longitudinally folded when at rest; with at most one closed, submarginal cell (1R1); cross-vein *2m-cu* absent. Hind wing with costa only, no closed cells; jugal lobe present. Mid and hind coxae each with annular constriction; inner surfaces of hind coxae without grooves or notches; trochantellar groove absent; hind leg with trochantellus; legs slender; tarsal claws bidentate. Metasoma short, separated from metanotum by at least the anterior width of T2; T2 and S2 fused to form cylindrical petiole; T2 and T3 freely articulating; 3rd–9th abdominal segments strongly, laterally compressed, blade-like; cerci absent; ovipositor concealed. Integument of mature larva with minute setae; mandible 3-toothed. Cocoon absent.

Evaniids are solitary parasites of the oothecae of blattid and blattellid cockroaches (V. K. Brown 1973). Adults are seen on flowers or searching on tree trunks or in litter for hosts. As adults walk their petiolate metasoma is moved up and down like a flag or hatchet.

The family is cosmopolitan, but more diverse in warmer regions. Australian evaniids are morphologically uniform although the wing venation is reduced (cells 1R1 and M lost) in one small species from North Qld. Species are mostly dark coloured, although a few are wholly or partially red-brown or have conspicuous, silver pubescence. [Hedicke 1939]

**13. Aulacidae** (Fig. 42.18E). Slender bodied (5–45 mm). Antennae 13-segmented in males, 14-segmented in

females. Mouth-parts not elongate. Pronotum reaching posteriorly to tegula, with or without distinct pronotal lobe; prepectus absent; pronotum and mesepisternum abut. Metasternum with bilobed process between hind coxae. Fore wing not longitudinally folded when at rest; with at most 3 closed, submarginal cells (1R1, 1Rs, 2Rs); cross-vein *2m-cu* usually present. Hind wing with costa and sometimes some additional longitudinal veins but without closed cells; jugal lobe absent. Coxae without annular constrictions; inner surface of hind coxa of female with groove or notch; hind trochanter with trochantellar groove; hind leg with trochantellus, although this sometimes weakly defined; legs slender; tarsal claws with 1 or more teeth. Metasoma elongate, separated from metanotum by at least the anterior width of T2; T2 and S2 not fused; T2 and T3 fused; cerci present; ovipositor exerted, often longer than metasoma. Integument of mature larva with minute setae; mandible 1-toothed; paired, sclerotised processes projecting from epistoma onto frontal area. Cocoon present.

Species of this small, cosmopolitan family parasitise the wood-boring, immature stages of Xiphydriidae and Coleoptera. During oviposition the metasoma is raised and the ovipositor directed anteroventrally so that the valves pass between the hind coxae. The valves pass through a guide formed by apposed notches or grooves on the inner surfaces of the hind coxae. The hind coxae are similarly modified to brace the ovipositor in *Certonotus* (Ichneumonidae) which also parasitise larvae tunnelling in wood and have the articulation of the metasoma remote from the hind coxae.

In Australia *Aulacus* (15 spp.) and *Pristaulacus* (16 spp.) have been reared from larvae or pupae of Cerambycidae and Buprestidae. Each tarsal claw has a single

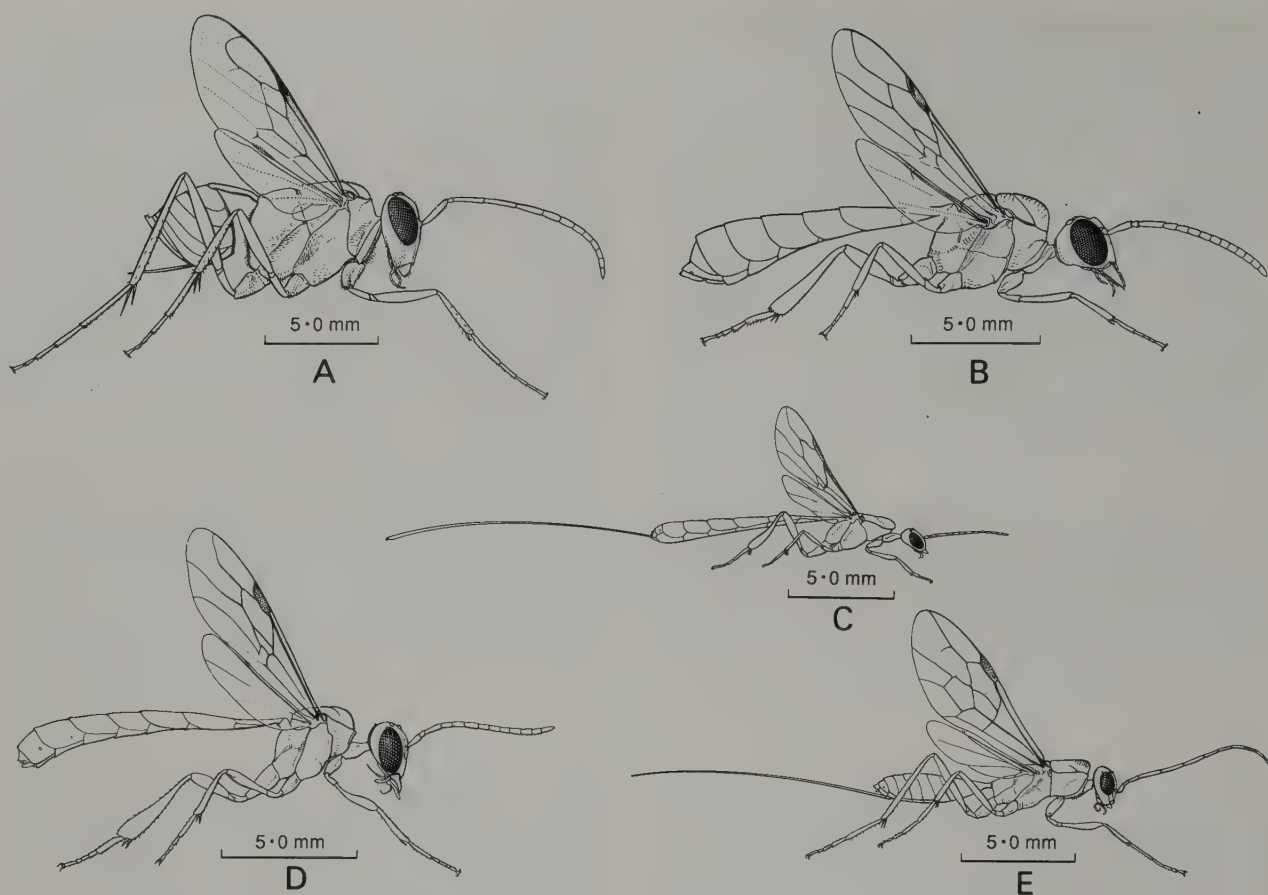


Fig. 42.18 Evanioidea: A, *Evania* sp., Evaniidae; B, *Aulacofoenus* sp., Gasteruptionidae; C, *Gasteruption* sp., Gasteruptionidae; D, *Eufoenus* sp., Gasteruptionidae; E, *Pristaulacus* sp., Aulacidae.  
[M. Quick]

tooth in *Aulacus* and 2 or more teeth in *Pristaulacus*. Both genera are cosmopolitan. [Crosskey 1953]

**14. Gasteruptionidae** (Figs 42.18B–D). Slender bodied (3.3–85 mm). Antennae 13-segmented in males (rarely 14), 14-segmented in females. Mouth-parts elongate. Pronotum reaching posteriorly to tegula, with distinct pronotal lobe; prepectus absent; pronotum and mesepisternum abut. Metasternum without bilobed process between hind coxae. Fore wing longitudinally folded when at rest; with at most 1 closed, submarginal cell (1R1); cross-vein *2m-cu* absent. Hind wing with costa only; jugal lobe absent. Coxae without annular constrictions; inner surfaces of hind coxae without grooves or notches; hind trochanter with or without trochantellar groove; hind leg with or without trochantellus; hind tibia swollen; tarsal claws with 1 tooth. Metasoma elongate, separated from metanotum by less than the anterior width of T2; T2 and S2 not fused; T2 and T3 fused; cerci present; ovipositor concealed or exserted, sometimes much longer than metasoma. Integument of mature larva with prominent setae, mandible 3-toothed. Cocoon present.

Gasteruptionids commonly are seen on flowers or hovering near bare ground, stumps, logs, trees or any other potential host nesting sites. Females of all species oviposit in nests of Apoidea or Vespidae. The gasteruptionid larva, after consuming the egg or larva of the host bee or

wasp, then eats the pollen or prey store of the host. If the partitions between cells in the nest are thin, the gasteruptionid larva may burrow into an adjacent cell and consume its contents as well (Malyshev 1968).

#### Key to the Subfamilies of Gasteruptionidae

- Mandibles long and broadly overlapping, usually with 2 broad, ill-defined teeth between basal tooth and apical tooth; trochantellus absent; apical sternum of ♀ not posteriorly incised; ovipositor not usually exserted ..... HYPTIOGASTRINAE  
Mandibles short and not broadly overlapping, with at most 1 tooth between basal tooth and apical tooth; trochantellus present or weakly indicated; apical sternum of ♀ posteriorly incised; ovipositor always exserted ..... GASTERUPTIONINAE

The HYPTIOGASTRINAE (Fig. 42.18B) include the most primitive gasteruptionids. The subfamily is most diverse in Australia but is also represented in South America, in New Zealand and on some other south-western Pacific islands. The ovipositor is concealed in all genera except *Hyptiogaster*. In several genera the hind legs are modified, with especially stout femora or tibiae or asymmetrically expanded tarsal segments. In females of *Crassifoenus* the



basal 4 tarsal segments of the hind leg are very short and bilobed and the apical segment and its claws are massively enlarged. In *Aulacofoenus* and *Eufoenus* the 2nd flagellar segment is shorter than the 1st. The hind trochanter has a distinct, transverse trochantellar groove in *Aulacofoenus* but not in *Eufoenus*. Known hosts are all ground nesting. *Hyptiogaster* (5 spp.; parasites of Masarinae) and *Crassifoenus* (2 spp.; parasites of Stenotritidae) are endemic. *Eufoenus* (20 spp.; parasites of Colletidae) occurs in Australia and on some south-western Pacific islands. *Aulacofoenus* (5 spp.) is known from Australia and South America.

The GASTERUPTIINAE (Figs 42.18C, D) include only the very large, relatively derived and almost cosmopolitan *Gasteruption*. The ovipositor is exerted in all species and can be 4–5 times as long as the metasoma. Known hosts of Australian *Gasteruption* (130 spp.) include ground-nesting Halictidae, Megachilidae and Hylaeinae (Colletidae) reoccupying abandoned nests of mud-dauber wasps, and Colletidae and Eumeninae (Vespidae) nesting in tunnelled or rotten wood. [Crosskey 1962b]

### Superfamily ICHNEUMONOIDEA

All ichneumonoids are parasitic or hyperparasitic. The scape is short and most species have numerous, closed cells in the fore wing, a trochantellus and a flexible metasoma often bearing a strongly exerted ovipositor. The superfamily is monophyletic with two autapomorphies: (1) The pronotum is modified with the prepectus fused to the posterior margin and recognisable only as a lobe

below the mesothoracic spiracle and an inflexed rim on the posterolateral edge of the pronotum (Gibson 1985). (2) S2 consists of a strongly sclerotised, anterior portion and a membranous, posterior portion (Fig. 42.19C) in which there are one or more weakly sclerotised sternites (Mason 1981). C and Sc of the fore wing are fused in most ichneumonoids, although a minute costal cell adjacent to the parastigma persists in some Braconidae. Often this remnant of the costal cell is heavily pigmented and resembles a second pterostigma. The antennae, usually long and multisegmented, are reduced in some small species, e.g. 13-segmented in some female Aphidiinae (Braconidae). Cerci are either digitiform, plate-like or absent.

T3 and T4 are joined rigidly in Braconidae and secondarily in some Ichneumonidae. The 2nd recurrent vein is lost from the fore wing of all Braconidae and a few Ichneumonidae. Cross-vein *r-m* in the hind wing of Ichneumonidae is at least slightly beyond the junction of R1 and Rs and cell R is longer than the submarginal vein. In Braconidae *r-m* arises at most slightly beyond the junction of R1 and Rs and usually before it, and cell R is always shorter than the submarginal vein.

The Apozygidae comprises a single Chilean species superficially resembling some doryctine Braconidae (Mason 1987).

Larvae have mandibles which are unidentate or with a row of numerous small teeth but never tridentate; maxillae and labium present or their sensilla arranged in discrete areas. Cocoon formed.

### Key to the Families of Ichneumonoidea Known in Australia

- Cell R in hind wing longer than submarginal vein (Figs 42.19A, B, D); 2nd recurrent vein present in fore wing (except in *Sathropterus*); T3 and T4 not rigidly joined ..... **Ichneumonidae** (p. 943)  
 Cell R in hind wing shorter than submarginal vein or absent (Fig. 42.20); 2nd recurrent vein absent from fore wing; T3 and T4 rigidly joined ..... **Braconidae** (p. 945)

**15. Ichneumonidae** (Fig. 42.19). Minute to very large (1.5–120 mm) solitary or gregarious parasites of larvae, prepupae and pupae of various endopterygote insects, spiders and spider egg sacs. Ovipositor often strongly exerted.

Adults are seen commonly at flowers, extrafloral nectaries and dew drops, especially in the early morning. Females search for hosts around tree trunks, logs, vegetation and in litter. Each female lays between 10 and several thousand eggs, sometimes near the host but more usually attached externally to the host cuticle (in which case the eggs may have special adhesive areas or hooks) or within the host's body (most commonly free in the haemocoel). After expulsion from the gonopore, eggs of Tryphoninae sometimes are retained at the base of the ovipositor, concealed by the apical sterna, or at the ovipositor tip. Too large for the lumen of the ovipositor, these eggs are attached to the ovipositor valves by stalks and pass down the outside of the ovipositor.

Almost certainly ichneumonids primitively attacked large hosts. Oviposition into eggs or small larvae is a

more specialised habit. Hosts in concealed places are sometimes paralysed. Eucerotinae have a planidial 1st instar larva. Ectoparasitic larvae tend to have a well-developed head capsule, papilliform antennae and strongly sclerotised, dentate mandibles. In endoparasitic larvae the head capsule is often reduced, the antennae are disc-like and the mandibles vestigial. A membranous, caudal vesicle, apparently derived from the mid gut, is present in some endoparasitic larvae, but occurs less commonly than in endoparasitic larvae of Braconidae. The larval head capsule provides some characters important to higher classification (Short 1978).

Pupation occurs either within the host's own pupation chamber or feeding recess, under bark, in litter or exposed on vegetation, in which case the ichneumonid larva spins an often hard cocoon. The cocoon is vestigial when endoparasites pupate within the remains of the host.

Ichneumonids favour moist habitats and are most diverse in the cool, wet, south-eastern parts of Australia. In drier regions they are most numerous near water-courses. There are relatively few species in arid, central

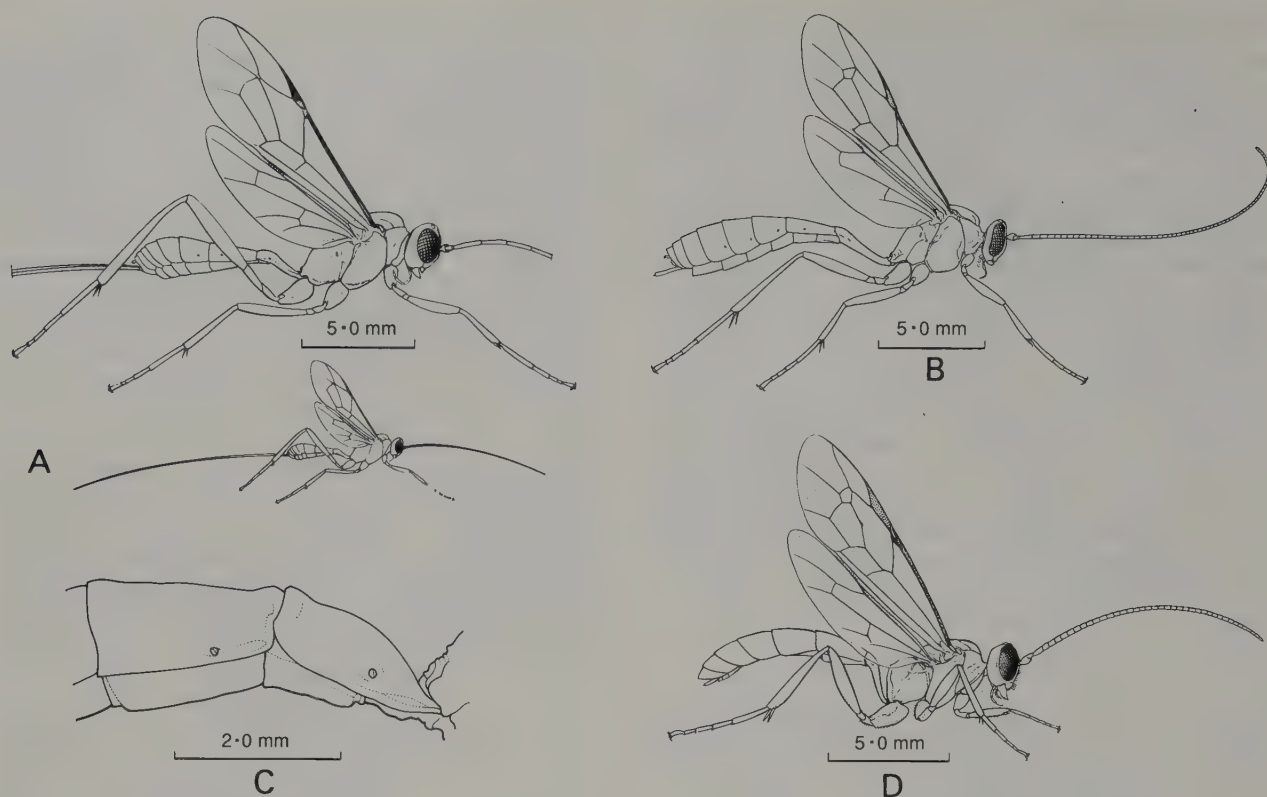


Fig. 42.19 Ichneumonidae: A, Phygadeuontinae; B, Ophioninae; C, Pimplinae, lateral view of anterior metasoma; D, Ichneumoninae.

[A, B, D by M. Quick; C by T. Nolan]

Australia although there the Cremastinae are particularly diverse and some species of Cremastinae and Ophioninae can be common.

The Australian ichneumonid fauna is not large compared with that of the Palaearctic, Nearctic, Neotropical or Afrotropical regions, probably reflecting both the geological history of the various regions, and the widespread aridity of present-day Australia. Cremastinae and Banchinae are unusually abundant in Australia. Species of these subfamilies tend to parasitise larvae which feed in concealed niches (e.g. in leaf rolls and mines) and such hosts are a feature of arid regions.

Gauld (1984a) provided keys to Australian subfamilies and genera and Gupta (1987) a catalogue to the Indo-Australian species.

Many Australian PIMPLINAE (63 spp.) are restricted to the tropical north-east and a number of genera and species are shared with New Guinea. Species are biologically relatively primitive, with either ecto- or endoparasitic larvae. Most Rhyssini and Ephialtini are ectoparasitic on insect larvae or pupae in concealed situations. Rhyssini are represented by *Megarhyssa nortoni* and *Rhyssa persuasoria*, both introduced to southern Australia from the Northern Hemisphere for biological control of *Sirex*, and *Epirhyssa bairoi* which occurs in northern Qld and New Guinea. Ephialtini are most common in tropical Qld although *Sericopimpla* (3 spp.) and *Zaglyptus* (1 sp.) include more widespread species. *Camptotypus* (5 spp.), with patterned bodies and mottled or darkened wings, resembles some

Braconinae and flies conspicuously in rainforest clearings. *Sericopimpla* oviposits through the silk produced by larvae of Lepidoptera. Extralimital species of *Zaglyptus* attack spiders with eggs in silk retreats. Pimplini parasitise immature Lepidoptera. The three species of *Echthromorpha* are all widespread outside Australia; they sometimes emit a pungent odour when handled. *Lissopimpla* (4 spp.) is commonly seen probing grass tussocks in search of prepupae or pupae of Lepidoptera. Males of *Lissopimpla* are attracted (largely by scents) to the female-mimicking flowers of terrestrial orchids (*Cryptostylis* spp.). Males protrude their claspers and attempt to copulate with the flowers. Pollinia attach to the wasp during this pseudocopulation and pollination occurs as wasps move from flower to flower. Bright yellow and black *Xanthopimpla* (17 spp.) are conspicuous in tropical areas. *Theronia* (5 spp., Delomeristini) are tropical, yellow-green parasites (or hyperparasites via other Pimplinae) of Lepidoptera. Polysphinctini (13 spp.) are ectoparasitic on spiders. [Gauld 1984b]

TRYPHONINAE (30 spp.) are ectoparasitic on large larvae of Lepidoptera or Symphyta. Reddish orange *Netelia* (20 spp.) is common, crepuscular or nocturnal, and females can inflict a painful sting.

LABENINAE (96 spp.) have many features plesiomorphic within the Ichneumonidae. Adults and larvae are morphologically primitive, larvae are ectoparasitic and many attack insects in wood. Mostly restricted to Australia and South America, the subfamily is almost certainly Gond-



wanan. *Certonotus* (23 spp.) and *Labena* (7 spp.) both occur in Australia and South America and parasitise larvae of Cerambycidae (COLE) or Siricidae in wood. *Poecilocryptus* (4 spp.) is endemic and associated with galls on *Eucalyptus* and *Acacia*. *Labium* (50 spp., especially in cooler regions) parasitises cells of solitary Apoidea, the wasp larva killing or eating the bee egg or larva and then feeding on the pollen store. *Brachycyrtus* (3 spp.) parasitises cocoons of Chrysopidae (NEUR) and *Adelphion* (6 spp.) spider egg sacs. [Gauld and Holloway 1986]

PHYGADEUONTINAE (295 spp.; Fig. 42.19A) is the largest subfamily with 57 Australian genera. Females generally search on foot for hosts. Most species are ecto- or endoparasitic on immature Lepidoptera, Hymenoptera and Neuroptera and pupate within the host cocoon. *Isdromas* (29 spp.) occurs in Australia, South America and Africa. *Meringops* (3 spp.) is known from Australia and Chile. Species of *Paraphylax* (53 spp.) have been reared from spider egg sacs, leaf mines of *Phylacteophaga* (Pergidae) and cocoons of various Lepidoptera. *Anacis* (55 spp.), *Xanthocryptus* (6 spp.) and the endemic *Ceratomansa* (7 spp.) parasitise Lepidoptera, while *Arthula* (2 spp.) attacks immature Vespidae. Females of *Gotra* (10 spp.) are sometimes seen searching for cocoons of Lepidoptera on bark. *Gelis* (1 sp.) females are commonly apterous.

XORIDINAE (3 spp.) presumably parasitise wood-boring Coleoptera.

ICHNEUMONINAE (121 spp.; Fig. 42.19D) are endoparasitic. Females search, generally on foot, for mature larvae or pupae of Lepidoptera in vegetation, litter or soil. Some species are sexually dichromic. *Ichneumon* (2 spp.) includes a common parasite of Noctuidae. *Gavrana* (26 spp.) also occurs in Indonesia and New Guinea. There are several small, endemic genera.

Extralimital EUCEROTINAE (9 spp.) oviposit on plants. The planidial 1st instar larva attaches to the exterior of a caterpillar to feed on haemolymph. The life cycle is completed only if the carrier caterpillar is parasitised by some other species of Ichneumonidae, in which case the eucerotine planidium enters the body of the other ichneumonid.

All Australian genera of CTENOPELMATINAE (29 spp.) are endemic. *Hypopheltes* (2 spp.), *Pergaphaga* (5 spp.) and *Westwoodia* (1 sp.) are endoparasitic on larvae of Pergidae but *Megaceria* (13 spp.) attacks immature Lepidoptera.

BANCHINAE (130 spp.) are endoparasitic on larvae of Lepidoptera. *Australoglypta* (18 spp.) is related to a South American genus. *Lissonota* (80 spp.) is most diverse in Vic. and Tas. *Philogalleria* (6 spp.) is endemic to southern Australia (Fitton 1987). *Apophua* (1 sp.), *Leptobatopsis* (4 spp.) and *Syzeuctus* (13 spp.) are primarily tropical.

Extralimital species of LYCORININAE (3 spp.) have been reared from Lepidoptera.

CAMPOPLEGINAE (89 spp.) are endoparasitic on larvae of Lepidoptera and Coleoptera, species often having narrow host ranges. Most genera occurring in Australia are

also present in the Oriental region. *Campoplex* (18 spp.), *Casinaria* (12 spp.) and *Delopia* (15 spp.) are the largest genera. *Venturia canescens* is a widespread parasite of *Ephestia kuehniella* (LEPI: Pyralidae) in stored grain.

OPHIONINAE (67 spp.; Fig. 42.19B) are endoparasitic on larvae of Lepidoptera, often being niche- rather than host-specific. Generally adults are pale coloured with large ocelli, nocturnal and attracted to light. *Enicospilus* (43 spp.) is circumtropical. Most *Dicamptus* (5 spp.) inhabit seasonally dry areas of northern Australia. *Leptophion* (7 spp.) also occurs in Indonesia, New Guinea and on Pacific islands. *Ophion* (5 spp.) favours cooler regions. *Riekophion* (3 spp.) and *Pamophion* (1 sp.) are endemic.

CREMASTINAE (128 spp.) are endoparasitic on larvae of small Lepidoptera and Coleoptera, especially those in concealed situations such as leaf rolls or mines. They are the most common ichneumonids in arid, central Australia. *Pristomerus* (50 spp.), *Temelucha* (55 spp.) and *Trathala* (13 spp.) are all cosmopolitan genera. *Dimophora* (9 spp.) is otherwise Holarctic. *Gahus* (1 sp.) is endemic.

TERSILOCHINAE (27 spp.) are most common in cool, damp habitats and are endoparasites of larvae of Coleoptera, especially Curculionidae and Chrysomelidae. Most Australian species belong to large genera with world-wide distributions.

PHRUDINAE (1 sp.) are endoparasites of larvae of Coleoptera.

MESOCHORINAE (23 spp.) are hyperparasitic on Braconidae, Ichneumonidae or Tachinidae (DIPT) within larvae of Lepidoptera, Coleoptera or Symphyta. *Mesochorus* (12 spp.) has been reared from Tachinidae parasitising larvae of paropsine Chrysomelidae (COLE).

ANOMALONINAE (32 spp.) are endoparasitic on larvae of Lepidoptera (e.g. *Heteropelma*, 4 spp.; *Habronyx*, 14 spp.; *Trichomma*, 5 spp.) or tenebrionid beetles (*Anomalon*, 3 spp.). Adults in flight have characteristically outstretched antennae, an elevated metasoma and splayed hind legs.

ACAEINITINAE (7 spp.) and HELICTINAE (20 spp.) are most common and diverse in moist, north-eastern areas. Extralimital helictines are endoparasitic on larvae of Mycetophilidae (DIPT). Australian ORTHOCENTRINAE (21 spp.) also probably parasitise Mycetophilidae.

DIPLAZONTINAE (5 spp.) are endoparasites of aphidophagous Syrphidae (DIPT). *Diplazon laetatorius* is cosmopolitan and one of the commonest ichneumonids.

METOPINAE (45 spp.) are endoparasites of larvae of Lepidoptera. Some brightly coloured adults apparently mimic eumenine Vespidae and buzz when disturbed.

The small subfamilies Adelognathinae, Agriotypinae, Orthopelmatinae, Stilbopinae, Neorhacodinae, Collyrinae and Paxylommatinae are absent from Australia.

**16. Braconidae** (Plate 6, Z, ZB; Figs 42.20, 21). Minute to large (1–80 mm) solitary or gregarious parasites of immature or, rarely, adult stages of various insects. Females usually attack larvae but some oviposit into eggs and development is delayed until the host larva is nearly mature.

Van Achterberg (1976b) and Tobias (1975) provided keys to most subfamilies. Shenefelt (1969–1980) and

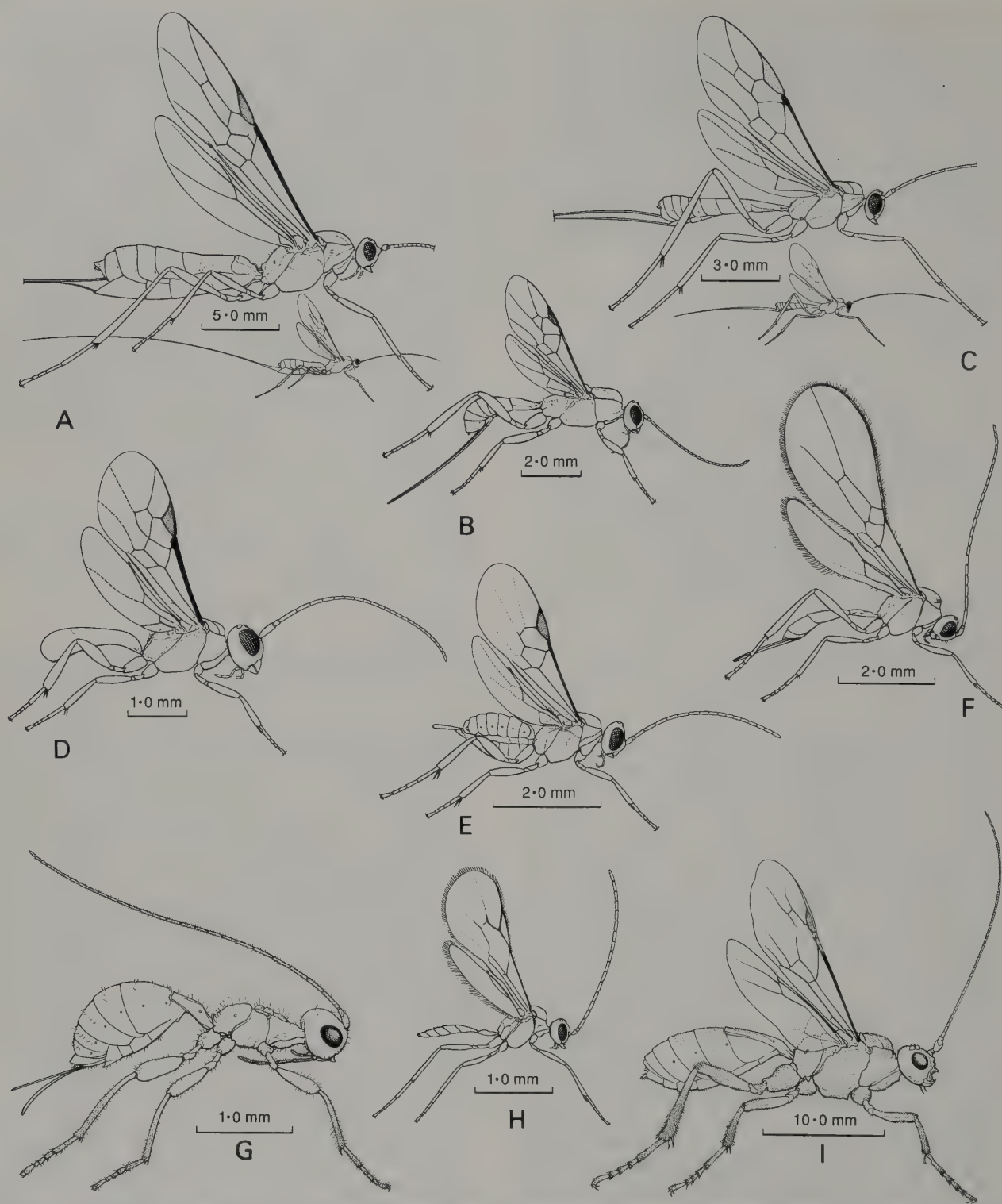


Fig. 42.20 Braconidae: A, *Virgulibracon* sp., Braconinae; B, Helconinae; C, Macrocentrinae; D, Cheloninae; E, Microgasterinae; F, Alysiinae; G, *Spathius* sp., Doryctinae; H, Aphidiinae; I, *Cercobarcon* sp., Cercobarconinae. [A–F, H by M. Quick; G, I by T. Nolan]

Shenefelt and Marsh (1976) have catalogued the world fauna.

Ancestral Braconidae most likely were ectoparasitic on larvae of Coleoptera in wood, but endoparasitism has evolved several times within the family (van Achterberg 1984) and the host range of modern subfamilies is wide

(R. W. Matthews 1974). Endoparasitic Braconidae sometimes have an additional, final, ectoparasitic feeding stage, and many pupate outside the host remains. Possibly there are two phylogenetic lines within the family: in one, the endoparasitic, early larval instars have acquired a caudal vesicle, a rectal evagination which disappears in later



instars, and the venom reservoir associated with the adult ovipositor is simple and thin walled; in the other line, larvae lack the rectal evagination, but adults have developed a well-muscled venom reservoir wall.

Four small subfamilies are endemic to Australia: Mesostoinae (1 sp.), Cercobarconinae (5 spp.), Trachypetinae (1 sp.) and Betylobracninae (3 spp.). The following subfamilies, each monotypic or with few species, are extralimital: Telengaiinae, Vaepellinae, Ypsistocerinae, Histeromerinae, Dirrhopinae, Ichneutinae, Meteorideinae, Xiphozelinae, Amicrocentrinae, Neoneurinae, Cenocoeliinae and Encominae.

### Key to the Subfamilies of Braconidae Known in Australia

by C. VAN ACHTERBERG

1. Exodont, i.e. mandibles with 3 or 4 teeth or lobes, usually directed outwards, their tips not touching when closed (Figs 42.21D, E) ..... ALYSIINAE  
Endodont, i.e. mandibles with 1 or 2 teeth, curved inwards, their tips touching when closed (Figs 42.21F, G) ..... 2
- 2(1). Mesoscutum strongly protruding above pronotum (Fig. 42.21A); cross-vein in hind wing between M+CuA and 1A absent ..... MESOSTOINAE  
Mesoscutum not or hardly protruding above pronotum (Fig. 42.20); or if protruding then cross-vein in hind wing between M+CuA and 1A present ..... 3
- 3(2). Antennal sockets joined by transverse sulcus ..... BETYLOBRACNINAE  
Transverse sulcus absent ..... 4
- 4(3). Hypoclypeal depression wide and deep, middle or apparent ventral margin of clypeus distinctly above upper level of mandibular bases (Fig. 42.21F, 'cyclostome subfamilies') ..... 5  
Hypoclypeal depression usually absent; if present then rather shallow, narrower, and medioventral margin of clypeus close to upper level of mandible bases ..... 7
- 5(4). Occipital carina absent; *m-cu* of hind wing absent; CuA of hind wing more than 2 times longer than M+CuA; dorsope absent; T2 usually strongly flattened laterally unless lateral parts largely membranous or T2 fused to T3; T3 and T4 sclerotised dorsally ..... BRACONINAE  
Either occipital carina present, *m-cu* of hind wing present (sometimes only as a pigmented line), CuA of hind wing less than 2 times longer than M+CuA or dorsope large and deep; T2 not flattened laterally, or if more or less flattened laterally then T3 and T4 largely membranous dorsally ..... 6
- 6(5). Fore tibia with longitudinal row of usually stout pegs or spines, or hind coxa with anteroventral tubercle ..... DORYCTINAE  
Fore tibia without row of pegs or spines; hind coxa without tubercle ..... ROGADINAE
- 7(4). Spiracles of T2 in weakly sclerotised areas on either side of sclerotised notum (Fig. 42.21B) ..... 8  
Spiracle of T2 in or near margins of strongly sclerotised notum ..... 10
- 8(7). Cross-vein between pterostigma and 2nd submarginal cell shorter than anterior length of cell; antennae 20–51-segmented ..... CARDIOCHILINAE  
Cross-vein longer than anterior length of 2nd submarginal cell (Fig. 42.20E); antennae 14- or 18-segmented ..... 9
- 9(8). Antennae 14-segmented ..... MIRACINAE  
Antennae 18-segmented ..... MICROGASTERINAE
- 10(7). Marginal cell of fore wing long and narrow; CuA<sub>2</sub> of fore wing absent ..... AGATHIDIINAE  
Marginal cell of fore wing shorter, wider; CuA<sub>2</sub> of fore wing present or absent ..... 11
- 11(10). T2 immovably joined to T3, forming with T4 a flat shield covering about 3/4 of the metasoma ..... ADELIINAE  
T2 flexibly joined to T3; if immovably joined then 3 basal tergites form convex shield, covering most of the metasoma ..... 12
- 12(11). Mesosoma with ventral, transverse carina immediately anterior to mid coxae ..... CHELONINAE  
Mesosoma without ventral, transverse carina immediately anterior to mid coxae ..... 13
- 13(12). Outer surfaces of hind trochantelli with pegs ..... MACROCENTRINAE  
Hind trochantelli without pegs ..... 14
- 14(13). Cross-vein between M+CuA and 1A of hind wing appendiculate (Fig. 42.20I) ..... 15  
Cross-vein between M+CuA and 1A of hind wing not appendiculate, sometimes absent (Fig. 42.20H) ..... 17
- 15(14). Rs+M of fore wing incomplete (Fig. 42.20I); face with medial projection ..... CERCOBARCONINAE  
Rs+M of fore wing complete; face without projection ..... 16
- 16(15). T2 more than 1.5 times longer than wide; T2 nearly tubular basally; propodeal spiracle slit-shaped, more than 3 times longer than wide ..... TRACHYPETINAE  
T2 less than 1.2 times longer than wide; T2 not tubular basally; propodeal spiracle sub-circular, less than 1.5 times longer than wide ..... SIGALPHINAE
- 17(14). Cross-vein between M+CuA and 1A of hind wing absent (Fig. 42.20H); scutellar sulcus smooth ..... APHIDIINAE  
Cross-vein usually present (Fig. 42.20B); if indistinct or absent, then scutellar sulcus crenulate ..... 18
- 18(17). Mesopleuron without anterior, vertical carina ..... 19  
Mesopleuron with anterior, vertical carina ..... 20
- 19(18). Labial palp 3-segmented; T3 usually with basal elevated area; vein M+CuA of fore wing sclerotised ..... GNAMPTODONTINAE  
Labial palp 4-segmented; T3 without basal elevated area; basal half of vein M+CuA of fore wing often unsclerotised ..... OPIINAE
- 20(18). T2 petiolate; spiracle of T2 usually at or behind midpoint of tergite ..... EUPHORINAE (pt)  
T2 sessile; spiracle usually anterior to midpoint of T2 ..... 21
- 21(20). Laterope deep; 2nd submarginal cell of fore wing open ..... EUPHORINAE (pt)  
Laterope shallow or absent; if deep then 2nd sub-

- marginal cell of fore wing closed ..... 22
- 22(21). Dorsal carinae of T2 curved anteriorly, along the more or less developed dorsope; CuA<sub>2</sub> of fore wing usually absent and apical half of 2nd intercept of 1A unsclerotised ..... BLACINAE
- Dorsal carinae meet at sides of T2 to form acute angle or carinae absent, dorsope absent or nearly so; if intermediate then CuA<sub>2</sub> and apical half 2nd intercept of 1A of fore wing both distinct, sclerotised ..... 23
- 23(22). Scutellum without any depression posteriorly ..... ORGILINAE
- Scutellum with transverse, crenulate depression posteromedially ..... 24
- 24(23). Pronotum with median dorsal pit and without antescutellar depression; apex of antenna without spine; mid lobe of mesoscutum without horizontal portion anteriorly ..... HELCONINAE
- Pronotum without median dorsal pit but with antescutellar depression; apex of antenna usually with spine, if absent then mid lobe of mesoscutum anteriorly with a narrow horizontal part ..... HOMOLOBINAE

DORYCTINAE are ectoparasitic on larvae of wood-boring and bark-mining Coleoptera. *Syngaster* has been reared from *Phoracantha* (Cerambycidae), *Monolexis* from *Lyctus brunneus* (Lyctinae). *Spathius* includes micropterous species (Fig. 42.20G). Some species are very large (body length 1.5–30 mm), the females having elongate ovipositors. [Fischer 1981]

ROGADINAE are predominantly endoparasites of larvae of Lepidoptera. In Australia *Aleiodes* has been reared from *Heliocoverpa*, *Persectania ewingii* and *Mythimna convecta* (all Noctuidae). Adults sometimes come to light. *Cystomastax* has conspicuously darkened wings.

Many BRACONINAE (Plate 6, Z, ZB; Figs 42.20A, 21C) are large (body length 1.4–80 mm), often with yellow-banded or dark wings, and black and orange bodies (e.g. *Iphiaulax*). They give off a characteristic odour when handled or disturbed. *Callibracon* parasitises *Phoracantha* (COLE: Cerambycidae), *Pycnobracon* larvae of cryptocephaline Chrysomelidae (COLE), and *Virgulibracon* larvae of Cossidae (LEPI) in wood. Other genera have been reared from larvae of various Lepidoptera, Symphyta and a few dipterous, chalcidoid and psyllid galls. [Quicke 1987]

The monotypic subfamily MESOSTOINAE (Fig. 42.21A) is known only from south-western W.A.

OPIINAE parasitise larvae of Diptera. In Australia hosts include leaf-mining Agromyzidae and many Tephritidae in fruit. [Fischer 1978]

Exodont mandibles assist ALYSIINAE (Fig. 42.20F) to escape from the puparia of host Diptera. Alysiini (cross-vein *r-m* present in fore wing) include *Asobara persimilis*, a parasite of *Drosophila melanogaster* and *Aphaereta aotea*, introduced from New Zealand to parasitise a variety of dung-breeding flies; *Alysia manducator*, introduced from Europe, appears not to have established. *Heratemis* from northern Qld has a spinose scutellum. *Aspilota* is sometimes reared from fungi. Dacnusiini (*r-m* absent in

fore wing) are less common than Alysiini. *Dacnusa* parasitises leaf-mining larvae of Agromyzidae and Platypzeidae. [Wharton 1980]

GNAMPTODONTINAE, ADELIINAE and MIRACINAE all parasitise tiny, leaf-mining larvae of Lepidoptera: *Gnamptodon* and *Adelius* larvae of Nepticulidae, *Mirax* larvae of Phyllocnistinae.

APHIDIINAE (Fig. 42.20H) parasitise aphids; several species of *Aphidius* and *Trioxy*s have been introduced as bio-control agents. *Parephedrus relictus* attacks *Taiwanaphis* on *Nothofagus*. [Carver and Stary 1974; Stary 1970, 1987]

HELCONINAE are diverse parasites of larval Coleoptera. *Trichiohelcon* has been reared from tunnels of Cerambycidae. In *Triaspis* and *Schizoprymnus* the first 3 metasomal terga form a carapace. BLACINAE also parasitise larvae of Coleoptera (van Achterberg 1976a).

In the EUPHORINAE *Meteorus* parasitises larvae of Lepidoptera and *Eadya* the immature stages of paropsine Chrysomelidae (COLE), but all other genera parasitise adult insects. In Australia *Perilitus* has been reared from morabine Eumastacidae (ORTH), *Dinocampus* from Coccinellidae (COLE), *Microctonus* from leptopiine Curculionidae (COLE) and *Syntretus* from Anthophoridae. In *Leiophron* Rs is close to the pterostigma in the fore wing as in most Proctotrupidae. In *Stenothremma* the suture between petiolar tergum and sternum has been obliterated. [S. R. Shaw 1985]

CERCOBARCONINAE (Fig. 42.20I) all are very large (21–

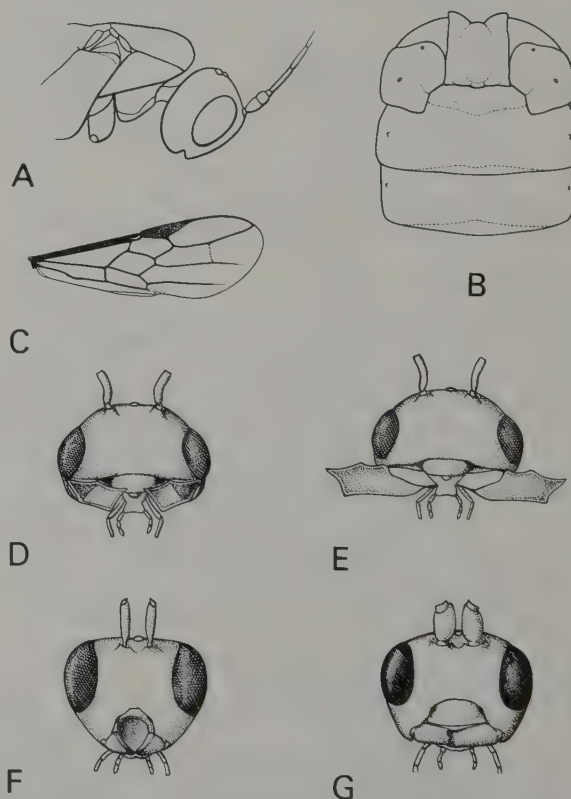


Fig. 42.21 Braconidae: A, Mesostoinae, anterior mesosoma, lateral; B, Microgasterinae, anterior metasoma, dorsal; C, Braconinae, fore wing; D–G, heads, frontal (D, E, exodont type; F, cyclostome type; G, normal type).

[A, C after van Achterberg 1976b; B by T. Nolan; D–G by S. Monteith]



27 mm) and brown to yellow, have large ocelli and resemble some Ichneumonidae. Species are nocturnal in arid regions. The single species of *Trachypetus* (TRACHYPETINAE) is also large (15–20 mm) and superficially similar to Cercobarconinae.

HOMOLOBINAE are generally pale coloured, with a short ovipositor, and are commonly nocturnal. Species are endoparasitic on larvae of Noctuidae and Geometridae (LEPI) which feed in the open at night. [van Achterberg 1979]

SIGALPHINAE oviposit in the eggs of Lepidoptera and develop within the growing host larvae.

AGATHIDIINAE are solitary or gregarious endoparasites of larvae of Lepidoptera. *Bassus* and *Agathis* attack various, cryptically-feeding larvae. Adults often resemble Braconinae in colour: *Cremnops*, *Disophrys* and *Zelomorpha* often are dark with yellow or orange bands.

MACROCENTRINAE (Fig. 42.20C) are endoparasitic on larvae of Lepidoptera and some are nocturnal. Species are slender and often large (length 4–35 mm), yellow-brown and with long ovipositors.

*Betylobrakon waterhousei* (BETYLOBRACONINAE) is known only from north-eastern Qld.

ORGILINAE include an *Orgilus* parasitic on the potato moth, *Phthorimaea operculella* (Gelechiidae).

CHELONINAE (Fig. 42.20D) are solitary endoparasites of larvae of Lepidoptera. Adults oviposit into host eggs but development is delayed until the host reaches its last larval instar. *Phanerotoma* and *Phanerotomella*, in which sutures persist in the metasomal carapace, frequently are attracted to light in tropical regions. *Ascogaster* and *Chelonus* lack sutures in the carapace. In females of *Megascogaster* the carapace is acuminate posteriorly.

*Cardiochiles* (CARDIOCHILINAE), with dark or patterned wings, is predominantly tropical.

MICROGASTERINAE (Figs 42.20E, 21B) are endoparasitic on larvae of Lepidoptera. Oviposition is into the egg or early larval instar. Pupation takes place outside the host, gregarious species often spinning their cocoons together in a silken web. Dark, dull-coloured species of *Apanteles* s.l., in which the 2nd radio-medial cell of the fore wing is open, are among the most common Braconidae.

*Protomicroplitis*, with a closed second radio-medial cell, attacks large larvae of Noctuidae. [Mason 1981]

### Superfamily PROCTOTRUPOIDEA

Parasitic. Antennae variable, subantennal groove absent. Antennal sockets and clypeus widely (or rarely narrowly) separated. Pronotum ventrally continuous behind fore coxae in Proctotrupidae, Pelecinidae and Vanhorniidae. Prepectus present but concealed beneath the posterolateral edge of the pronotum in Monomachidae, Roproniidae and Austroniidae; prepectus fused to posterior of pronotum in all other families and represented only by posterior pronotal inflection. Mesoscutum without median sulcus. Axillae variable. In fore wing of species with fully developed wings, pterostigma either present or absent, radial cell usually defined posteriorly (at least by coloured streak) and costal cell usually present. In hind wing M+CuA usually at least weakly indicated. Suture between T2 and S2 usually absent. Metasomal spiracles usually present; cerci variable. The ovipositor is usually concealed within the metasoma; if elongate it is sometimes accommodated in an anteroventral diverticulum of one of the metasomal sterna, in an external gutter or in an enlarged apical sternum. Few larvae are known.

There are no autapomorphies for the superfamily. The Heloridae and Peradeniidae are sister groups. The Monomachidae and Diapriidae, both parasitic or predominantly parasitic on Diptera and both with T2 and S2 fused to form a petiole, may be closely related. The metasoma is similar in Austroniidae and Roproniidae. Of the nine proctotrupoid families only three have more than ten species world-wide. Probably the proctotrupoid families, several of which retain wing venation and metasomal segmentation relatively plesiomorphic within the Apocrita, are isolated remnants of an ancient radiation of the parasitic Hymenoptera. Peradeniidae and Austroniidae are endemic to Australia. Vanhorniidae (parasitic on larvae of Eucnemidae in wood) and Roproniidae (parasitic on larvae of Symphyta) are Holarctic and Oriental, and Pelecinidae (parasites of larvae of Scarabaeidae in soil or wood) are restricted to the Nearctic and Neotropical regions. [Naumann and Masner 1985]

### Key to the Families of Proctotrupeidea Known in Australia

1. Inner margins of compound eyes strongly convergent ventrally; in lateral view pronotum with sharp, concave, re-entrant declivity (Fig. 42.22j) ..... **Peradeniidae** (p. 950)
- Inner margins of compound eyes not convergent ventrally; in lateral view pronotum convex and produced forward ..... 2
- 2(1). T3 subequal to T4 in length (Figs 42.22A, B, I) ..... 3
- T3 considerably longer than T4 (Figs 42.22C, F–H, K–M) ..... 4
- 3(2). Metasoma elongate, petiole at least 3 times longer than wide (Figs 42.22A, B); ovipositor not externally visible at rest; tarsal claws simple ..... **Monomachidae** (p. 950)
- Metasoma short, petiole at most twice as long as wide (Fig. 42.22i); ovipositor arising subapically; tarsal claws each with a basal, rectangular lobe ..... **Austroniidae** (p. 952)
- 4(2). Scape elongate, at least 2.5 times as long as wide (Figs 42.22C, F–H); antennal shelf usually distinct; pterostigma absent ..... **Diapriidae** (p. 950)
- Scape short, at most 2.2 times as long as wide (Figs 42.22K–M); antennal shelf absent; pterostigma present ..... 5
- 5(4). Antennae 13-segmented; transscutal articulation absent; median cell of fore wing not defined, basal intercept of Rs+M absent (Figs 42.22K, L) ..... **Proctotrupidae** (p. 952)
- Antennae 16-segmented, including anellus; transscutal articulation present; median cell of fore wing defined, basal intercept of Rs+M present (Fig. 42.22M) ..... **Heloridae** (p. 950)



**17. Monomachidae** (Figs 42.22A, B). Small to medium sized (6–15 mm); antennae 15-segmented in females, 14-segmented in males; retaining relatively well-developed wing venation; trochantellus present; T2 and S2 fused to form petiole; metasoma posteriorly slender, tapering in females, blunt in males; cerci digitiform.

*Monomachus* (3 spp.) occurs in moist forests and gardens in the east and south-west where adults are common in cooler months. Females oviposit into the eggs of *Boreoides* (DIPT: Stratiomyidae) and adult wasps emerge from mature host larvae or puparia, the relatively small, male hosts each yielding one parasite, the larger, female hosts several. The family also occurs in New Guinea and the Neotropical region. [Naumann 1985]

**18. Diapriidae** (Figs 42.22C–H). Small (1–6 mm). Antennae usually 9–15-segmented in females, 12–14-segmented in males, and usually inserted remote from clypeus on a prominent, frontal shelf; wing venation reduced; trochantellus present; T2 and S2 fused to form petiole; T3 and S3 or S4 large; cerci digitiform or plate-like. Sexual dimorphism often marked.

Most Diapriidae are endoparasitic on prepupae or pupae of Diptera. Adults are most common on low vegetation in moist, shaded habitats, in areas of high rainfall. Females search for hosts in litter and soil, sometimes flying very little. Often wings are reduced or absent, especially in females. De-alated or wing-reduced adults of some genera are associated with ants or termites, and an extralimital species has been reared from cocoons of Formicidae. Ismarinae parasitise Dryinidae, and extralimital Diapriinae have been recorded from immature Coleoptera.

#### Key to the Subfamilies of Diapriidae

1. Gastral terga with sharp lateral margins, abruptly reflexed; S3 much shorter than S4 (Fig. 42.22E) ..... AMBOSITRINAE
- Gastral terga laterally rounded, not abruptly reflexed; S3 much longer than S4 (Fig. 42.22D) ..... 2
- 2(1). Antennae inserted low on face, near clypeus, frontal prominence not developed; hind tibiae apically strongly enlarged (Fig. 42.22G); cerci not in depressions ..... ISMARINAE
- Antennae inserted high on face, on distinct frontal prominence; hind tibiae not strongly enlarged (Figs 42.22C, F); cerci inserted in depressions or not well developed ..... 3
- 3(2). Antennae of ♀ with 14–15 (rarely 12–13) segments, without abrupt club; antennae of ♂ with 14 segments, with 1st flagellar segment carinate; T3 anteriorly not overlapping posterior of petiole ..... BELYTINAE
- Antennae of ♀ with 11–13 (rarely 14) segments, often with more or less abrupt club; antennae of ♂ with 13 or 14 segments, with 2nd (rarely 1st) flagellar segment carinate; T3 anteriorly at least partially overlapping posterior of petiole ..... DIAPRIINAE

The subfamily BELYTINAE (50 spp.) includes some of the most plesiomorphic Diapriidae. No Australian species have been reared but extralimital species parasitise

Mycetophilidae. *Belyta* (20 spp.), with a forked, median, propodeal carina, is cosmopolitan; *Stylaclista* (9 spp.; Fig. 42.22F), in which females have a 'beaded' tail, occurs also in New Zealand and Melanesia; and *Psilommella* (1 sp.) with a wrinkled scutellum, is endemic. Many species cannot be assigned to described genera. One undescribed genus with large, hind tibial spurs, occurs also in New Zealand and South America.

The subfamily AMBOSITRINAE (50 spp.) has a Gondwanan distribution, with only a few genera extending into Melanesia and the Nearctic region (Naumann 1982, 1987a, 1988). *Pantolytomyia* (1 sp.), with an anteriorly incised 1st gastral tergite, and *Diphoropria* (26 spp.; Figs 42.22E, H), in which the 1st gastral tergite is anteriorly emarginate, are also represented in New Zealand. *Scianomas* (3 spp.), with a pronotal scrobe, is similar to New Zealand and South American genera. The fore wings are patterned in *Austroxylabis* (1 sp.), and parchment-like with a transverse fold in *Acanthobetyla* (11 spp.). New Zealand ambositrines have been reared from Mycetophilidae (DIPT).

ISMARINAE (*Ismarus*, 2 spp.; Fig. 42.22G) are unusual among Apocrita in having a false, second fore tibial spur. Holarctic species are hyperparasitic on immature Dryinidae developing ectoparasitically on Cicadellidae (HEMI). [Masner 1976b]

Most DIAPRIINAE (220 spp.) belong to the cosmopolitan genera *Basalis* (40 spp.), *Spilomicrus* (40 spp.), *Trichopria* (45 spp.), *Idiortya* (13 spp.), *Entomacis* (13 spp.), *Paramesius* (5 spp.) and *Diapria* (1 sp.). *Neurogalesus* (15 spp.), with a grotesque, opisthognathous head, extends into the Oriental region. Several undescribed genera are shared with the Oriental or Afrotropical regions. *Hemilexomyia* (1 sp.; Figs 42.22C, D) occurs also in New Zealand. *Leaiopria* (2 spp.), from nests of *Nasutitermes* (ISOP: Termitidae) (Naumann and Masner 1980), *Austropria* (4 spp.), with wing-reduced females (Masner 1969c), and several undescribed genera are endemic. Australian species have been reared from puparia of Stratiomyidae, Syrphidae, Tephritidae, Calliphoridae, Sarcophagidae and Muscidae, from unidentified Diptera in fungi, and from Tachinidae which have pupariated after parasitising immature Pergidae. [Nixon 1980]

**19. Heloridae** (Fig. 42.22M). Small (4–5 mm); antennae 16-segmented, including an anellus; wing venation well developed with triangular median cell; trochantellus present on hind leg; T2 and S2 fused to form petiole; T3–5 fused to form syntergum, S3–6 form synsternum; cerci plate-like.

*Helorus* (1 sp.) is endoparasitic on larvae of Chrysopidae (NEUR) and emerges after the host has spun a cocoon. [Townes 1977b]

**20. Peradeniidae** (Fig. 42.22J). Small (4–8 mm); antennae 13-segmented in females, 12-segmented in males; pronotum with sharp, re-entrant declivity; wing venation reduced; trochantellus absent; T2 and S2 fused to form petiole; gaster and hind tibia pedunculate; T3–5 fused to form syntergum, S3–6 form synsternum, in females; syntergum and synsternum with incomplete sutures in males; cerci articulated but not protruding.



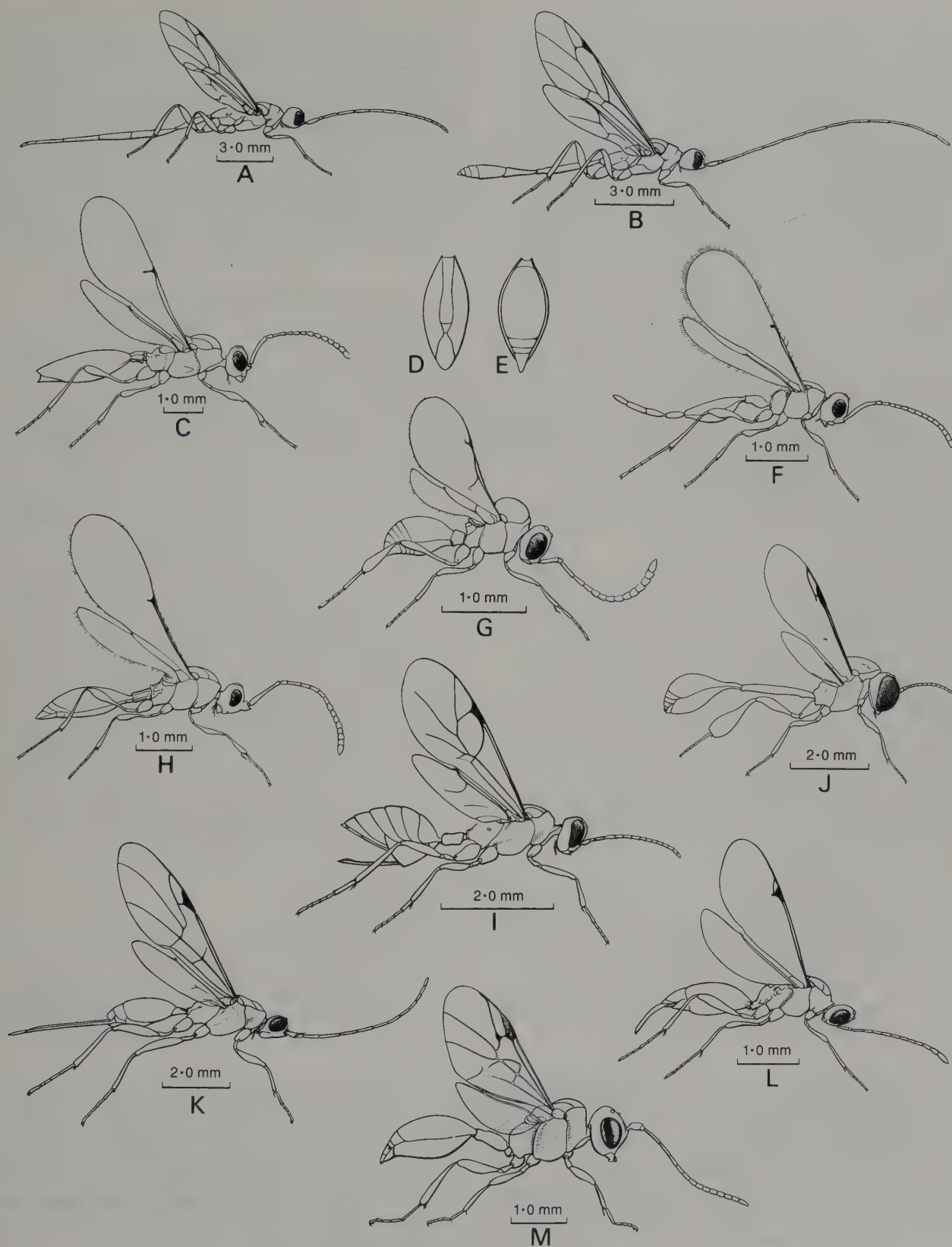


Fig. 42.22 Proctotrupeoidea: A, *Monomachus antipodalis*, Monomachidae, ♀; B, *M. antipodalis*, ♂; C, *Hemilexomyia* sp., Diapriidae-Diapriinae; D, gaster of *Hemilexomyia* sp., ventral; E, gaster of Diapriidae-Ambositrinae, ventral; F, *Stylaclista* sp., Diapriidae-Belytinae; G, *Ismarus* sp., Diapriidae-Ismarinae; H, *Diphoropria* sp., Diapriidae-Ambositrinae; I, *Austronia rubrithorax*, Austroniidae; J, *Peradenia clavipes*, Peradeniidae; K, *Austroserphus* sp., Proctotrupidae; L, *Oxyserphus* sp., Proctotrupidae; M, *Helorus australiensis*, Heloridae. [A–I, K, L by S. Monteith; J, M by A. Hastings]

This endemic family is known only from the south-east (including Tas.) where *Peradenia* (2 spp.) occurs in both moist forests and drier mallee areas. Hosts are unknown. [Naumann and Masner 1985]

**21. Austroniidae** (Fig. 42.22i). Small (4–6 mm); antennae 15-segmented in females, 14-segmented in males; wing venation relatively well developed, but without closed median cell; trochantellus present; T2 and S2 fused to form petiole; gaster laterally compressed; cerci digitiform; hypopygium deeply incised.

The family is endemic. *Austronia* (3 spp.) occurs in moist forests and heath in the south-east (including Tas.) and south-west. Hosts are unknown. [Riek 1955d; Naumann and Masner 1985]

**22. Proctotrupidae** (Figs 42.22k, l). Mostly small (3–15 mm); mesosoma without transscutal articulation; metasoma with a large syntergum; trochantellus sometimes present on fore leg; T2 and S2 (petiole) and synsternum fused; metasoma in females usually posteriorly down-curved and telescopic; cerci digitiform or absent. Most are solitary or gregarious endoparasites of larvae of Coleoptera, but some extralimital genera have been reared from Mycetophilidae (DIPT). Pupation occurs outside the host remains. Adults are swept commonly from low vegetation in moist, forest habitats.

*Austroserphus* (1 sp.; Fig. 42.22k) and *Acanthoserphus* (1 sp.) retain relatively well-developed wing venation with a large radial cell, and have a strong, apical spine on the scape. The female hypopygium is produced strongly in *Austroserphus* which occurs in the south-eastern mainland and Tas., and is very similar to *Austrocodrus* from southern South America. *Acanthoserphus*, in which the pronotum and metanotum are spinose, occurs in north-eastern Qld and New Guinea. In all other Australian genera the wing venation is reduced, with the radial cell reduced or almost obliterated. *Exallonyx* (3 spp.), in which the fore and mid tarsal claws each have a fine, black, basal tooth, and *Mischoserphus* (2 spp.) occur

world-wide. *Exallonyx trifoveatus* is a cosmopolitan parasite of Staphylinidae (COLE) in compost heaps. *Apoglypha* (5 spp.), which has a small radial cell, is endemic; one species has been reared from larvae of Erotylidae (COLE). The fore wing has an infusate cloud around the pterostigma and a small radial cell in *Serphonostus* (1 sp.) which is endemic to Tas. *Oxyserphus* (20 spp.; Fig. 42.22l) is exclusively Indo-Australian and parasitises Curculionidae and Anthribidae (COLE); the ocelli are greatly enlarged in a nocturnal species from northern Australia. [Townes and Townes 1981]

### Superfamily PLATYGASTEROIDEA

Parasites of eggs or larvae. Antennal sockets and clypeus very narrowly separated or contiguous. Scape relatively long (length more than 2.5 times width). Pronotum virtually continuous behind fore coxae; prepectus fused to posterior of pronotum and represented by posterior pronotal inflection. Mesoscutum without median sulcus. Axillae variable. Fore wing without pterostigma; costal cell present or absent and radial cell open posteriorly or absent. M+CuA absent from hind wing. Suture present between T2 and S2; metasomal spiracles absent. The ovipositor at rest is concealed within the metasoma but can be protruded by an increase in hydrostatic pressure within the metasoma. T9 is divided into anterior and posterior parts with the anterior part concealed and attached to the base of the tube-like ovipositor and the posterior part either exposed and bearing cerci or membranous and concealed. Sometimes the posterior part of T9 is carried subapically on the protruded ovipositor. In some species the ovipositor is extremely long and accommodated by anterodorsal or anteroventral diverticula of the metasoma. Some Scelionidae retain the most plesiomorphic wing venation and tibial spur formula in the superfamily.

First instar larvae are teleaform in Scelionidae and hymenopteriform or cyclopoid in Platygasteridae.

### Key to the Families of Platygasteroidea

1. T3 not the longest of all metasomal terga (Figs 42.23B–D, G), at most subequal to T4 ..... **Scelionidae** (pt, p. 953)
- T3 distinctly the longest of all metasomal terga (Figs 42.23A, E, F, H–K), several times longer than T4 ..... 2
- 2(1). Fore wing with stigmal and usually also postmarginal veins at least in ♂♂ (Figs 42.23A, E, H); antennae usually with 12 or 11, rarely 10 segments ..... **Scelionidae** (pt, p. 953)
- Fore wing without stigmal or postmarginal veins, often veinless (Figs 42.23I–K); antennae with 10 or fewer segments ..... **Platygasteridae** (p. 952)

**23. Platygasteridae** (Figs 42.23I–K). Minute to small (0.5–2.5 mm). Antennae of females 7–10-segmented, of males 8–10-segmented; scape elongate, more than 2.5 times longer than wide; scape and reflexed flagellum often forming Z-shape. Trochantellus present. Fore wing venation reduced to a knobbed, submarginal vein not attaining the costal margin or venation absent. Cerci absent. The family is most diverse in moist forests.

PLATYGASTERINAE (Figs 42.23I, K) are morphologically and biologically uniform. All parasitise larvae of Cecidomyiidae (DIPT) in galls and Australian species have been reared from leaf and stem galls on *Eucalyptus* and

*Acacia*. *Leptacis*, *Platygaster*, *Proplatygaster*, *Amblyaspis*, *Synopeas* and *Trichacis* have been recorded and there is an undescribed, endemic genus. Some extralimital *Platygaster* are polyembryonic. *Iphitrachelus* (2 spp.) is the only platygasterid genus with 4-segmented tarsi. In females of some species of *Inostemma* T2 has a horn-like, anterior projection; Australian species have been reared from galls (? cecidomyiid) on *Leptospermum*.

SCELIOTRACHELINAE have more diverse morphology and hosts. *Aphanomerella* (endemic; 1 sp.) parasitises eggs of Paropsina (COLE: Chrysomelidae). *Aphanomerus* (also represented in New Zealand; 8 spp.) attacks eggs of



Fulgoroidea (HEMI). The scape is shield-like in *Platygastoides* (25 spp.; Fig. 42.23j) which includes many wing-reduced, litter-frequenting species; the genus is restricted to moist forests in Australia and New Caledonia. There are several additional, endemic genera. *Parabaeus* and several other genera have essentially Gondwanan distributions, and *Aphanomerus* is represented only in Australia and New Zealand. Extralimital species of *Allotropa* and *Amitus* have been reared from Pseudococcidae and Aleyrodidae (HEMI) respectively. [Kozlov 1970; Masner and Huggert 1989]

**24. Scelionidae** (Figs 42.23A–H). Minute to small (0.5–7.5 mm) parasites of eggs of insects and spiders. Antennae 6–12-segmented (females) or 10–12-segmented (males) (14-segmented in some extralimital species); scape elongate, more than 2.5 times longer than wide. Trochantellus absent. Fore wing venation reduced, pterostigma absent. Cerci plate-like. Scelionidae occur in all terrestrial and fresh water habitats, especially in warmer regions. Most of the larger Australian genera are well represented worldwide or are shared with the Oriental, Melanesian or Afrotropical regions. [Masner 1976a, 1980]

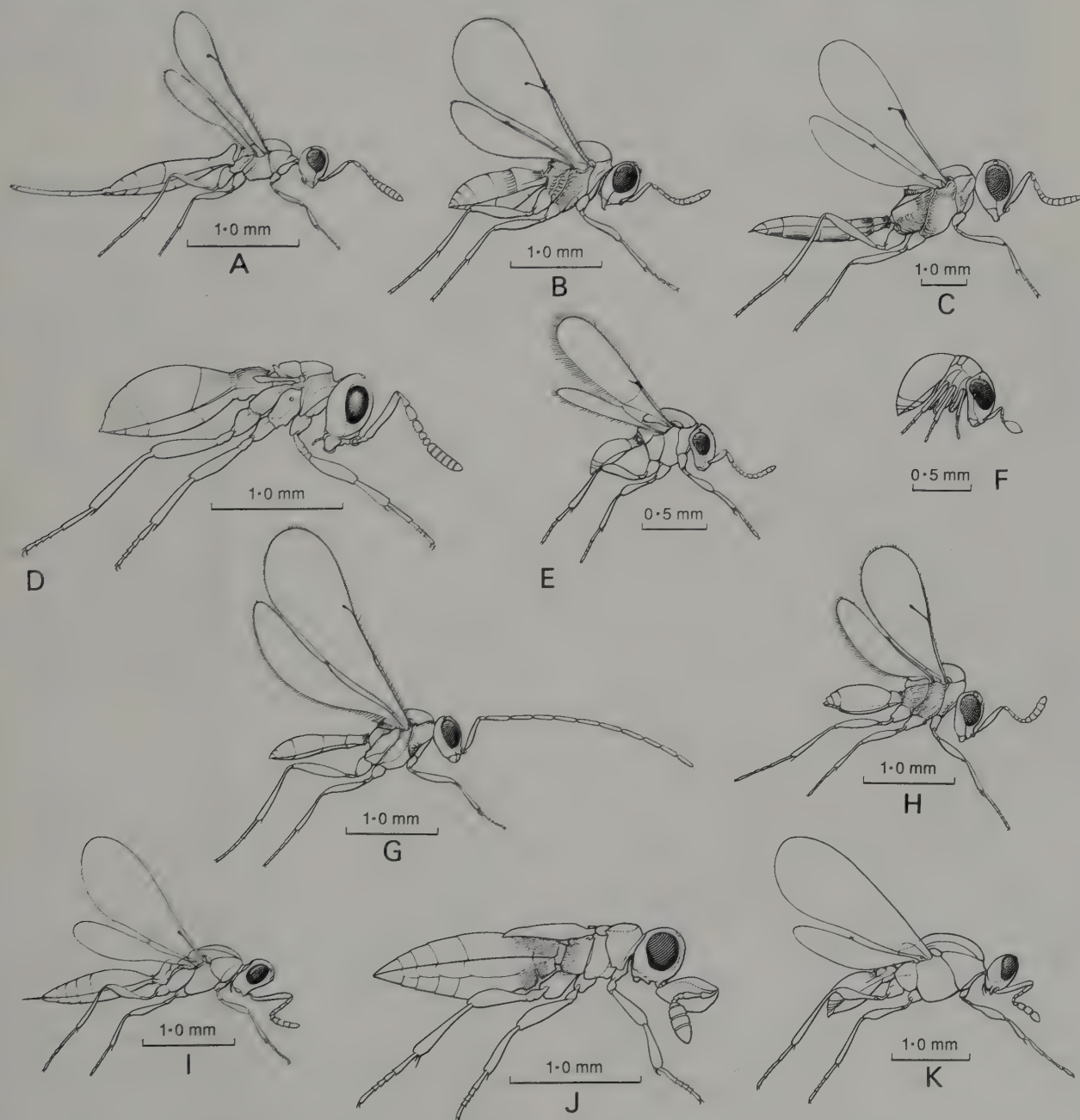


Fig. 42.23 Platygasteroidea: A, *Probaryconus* sp., Scelionidae-Scelioninae; B, *Hadronotus* sp., Scelionidae-Scelioninae; C, *Scelio* sp., Scelionidae-Scelioninae; D, *Trimorus* sp., Scelionidae-Teleasinae, ♀; E, *Baeus* sp., Scelionidae-Scelioninae, ♂; F, *Baeus* sp., ♀; G, *Trimorus* sp., Scelionidae-Teleasinae, ♂; H, *Trissolcus* sp., Scelionidae-Telenominae; I, unidentified Platygasteridae-Platygasterinae; J, *Platygastoides* sp., Platygasteridae-Sceliotrachelinae; K, unidentified Platygasteridae-Platygasterinae. [A–C, E–I, K by S. Monteith; D, J by T. Nolan]

## Key to the Subfamilies of Scelionidae

1. Metasoma without sharp, lateral margin, terga laterally loosely overlapping sterna; T3 larger than other metasomal terga (Fig. 42.23H); antennae of ♀ usually 11-, rarely 10-segmented, of ♂ 12-segmented ..... TELENOMINAE
- Metasoma with sharp, lateral margin, terga laterally sharply reflexed and closely attached to sterna; T3 rarely the largest; antennae of ♀ usually 12-, rarely 6–11-segmented, of ♂ usually 12-, rarely 8–11-segmented ..... 2
- 2(1). Lateral ocelli much closer to median ocellus than to compound eyes; T4 the largest metasomal tergum (Figs 42.23D, G); marginal vein several times longer than stigmal vein, postmarginal vein absent ..... TELEASINAE
- Lateral ocelli usually closer to compound eyes than to median ocellus; if closer to median ocellus then T4 not the largest metasomal tergum, or marginal vein shorter than stigmal vein and postmarginal vein long, or wings veinless or absent ..... SCELIONINAE

Most SCELIONINAE (310 spp.) parasitise the eggs of Orthoptera, Heteroptera and spiders. Scelionini parasitise Acrididae and adults of *Scelio* (32 spp.; Fig. 42.23C) are often abundant on locust egg beds. Baryconini (e.g. *Baryconus*, 10 spp.; *Bracalba*, 3 spp.; *Oxyscelio*, 14 spp.) parasitise eggs of Phaneropterinae (Tettigoniidae) on or in plants. Calliscelionini attack eggs of Gryllidae and Tettigoniidae: *Macroteleia* (4 spp.) and *Triteleia* (16 spp.) include some of the largest scelionids. *Probarryconus* (10 spp.; Fig. 42.23A), *Calliscelio* (8 spp.) and *Lisptoteleia* (9 spp.) are dominant genera. *Neoparidris* (1 sp.), *Crama* (2 spp.) and *Jarabambius* (1 sp.) are endemic genera. The hosts of Psilanteridini (11 genera), Doddliellini (*Doddiella*, 1 sp.) and the endemic Neoscelionini (*Neoscelio*, 5 spp.) are unknown. Cremastobaeini (*Cremastobaeus*, 4 spp.) parasitise cricket eggs. Extralimital species of Aradophagini (represented in Australia by *Ladora*, 3 spp.) are assumed to parasitise eggs of Aradidae. The monotypic tribe Mantibariini is represented by the cosmopolitan *Mantibaria anomala*; de-alated adult females are phoretic on Mantidae, feed on mantid haemolymph and oviposit into fresh oothecae. Platyscelionini (*Platyscelio*, 1 sp.) are extremely flattened and some extralimital species parasitise Phaneropterinae (Tettigoniidae). Gryonini attack eggs of various Heteroptera. *Gryon* (26 spp.) is one of the largest genera of Scelionidae world-wide. *Encyrtoscelio* (1 sp.), with a curious frontal shelf, parasitises eggs of Cydnidae in the soil.

Silk production is common to the hosts of both Embidobiini and Baeini. Embidobiini (*Embidobia*, 3 spp.) parasitise eggs of Embioptera. Baeini parasitise eggs of spiders and include the smallest scelionids. Females are often stout and wingless; males are usually winged. *Mirobaeoides* (12 spp.) is endemic and *Baeus* (3 spp.; Figs 42.23E, F) has a world-wide distribution. T2 is produced into a horn to accommodate the elongate, internal ovipositor mechanism in *Ceratobaeus* (23 spp.) and *Odontacolus* (3 spp.), but this tergite is flat in *Idris*

(27 spp.) and *Hickmanella* (2 spp.). Thoronini, which parasitise eggs of semiaquatic Heteroptera (Nepidae, Gerridae) are represented by *Tiphodytes* (1 sp.) and *Microthoron* (1 sp.). [Galloway and Austin 1984]

TELEASINAE (60 spp.) are closely related to the Scelioninae and parasitise eggs of Carabidae (COLE). Teleasini (e.g. *Trimorus*, 44 spp.; Figs 42.23D, G) are most commonly encountered in moist forests. Xenomerini are represented by *Xenomerus* (3 spp.). [Dodd 1930]

TELENOMINAE (75 spp.). The frons is conspicuously sculptured in *Trissolcus* (20 spp.; Fig. 42.23H) and *Psix* (7 spp.), which parasitise eggs of Heteroptera. *Trissolcus basalis* is reared commonly from eggs of Pentatomidae. The more weakly sculptured *Telenomus* (40 spp.) and *Phanuromyia* (6 spp.) are reared most commonly from eggs of Lepidoptera. [N. F. Johnson 1985, 1988]

## Superfamily CYNIPOIDEA

Endoparasitic or hyperparasitic on various insects, or associated with plant galls. Antennae of female usually 13-segmented, less commonly 12–19-segmented; male antennae usually 14–15-, less commonly 12–18-segmented, 3rd or 4th segment often elongate or curved; subantennal groove absent. Pronotum reaching to tegula. Prepectus fused to posterior of pronotum and represented by posterior pronotal inflection. Fore wing without costal cell; usually without pterostigma (retained in *Austrocynips*). Radial cell triangular or subtriangular. Mid tibia with 2 spurs. First metasomal segment forming petiole. Gaster laterally compressed, sterna small and mostly concealed by lateral panels of terga; apical sternum large. Ovipositor usually concealed. Spiracles present on T8; cerci either digitiform, plate-like or absent. First instar larvae polypodeiform or eucoiliform. Mature larvae with 2- or 3-toothed mandibles. Cocoon usually absent.

Many cynipoid families are defined more clearly by biological characteristics than on morphology. Almost certainly parasitism is the primitive life style and phytophagy is derived. Ibalidae retain many features plesiomorphic within the Cynipoidea (relatively well-developed wing venation and a simple pattern of gastral terga) and, as is the case with many other 'primitive' groups of parasitic Hymenoptera, are parasites of insects in wood. The wing venation is more reduced in other families. Eucoilidae and Charipidae, both well defined morphologically and with distinctive biologies, are each more homogeneous than is the Figitidae. The morphologically and biologically uniform Eucoilidae perhaps are most closely related to the Figitidae or a subfamily of Figitidae. Parasitic on Diptera and with numerous species world-wide, the Eucoilidae probably are a relatively recent radiation. Only the Eucoilidae and Charipidae are well represented in Australia. Gall-inhabiting Cynipidae, which are diverse in the Holarctic region, are almost absent from Australia where various Chalcidoidea are the dominant, gall-associated Hymenoptera. Alternation of generations and flightless adults are features of the life cycle of many extralimital Cynipidae. [Weld 1952; Königsmann 1978a; Quinlan 1979; Nordlander 1982, 1984; Fergusson 1986, 1988]



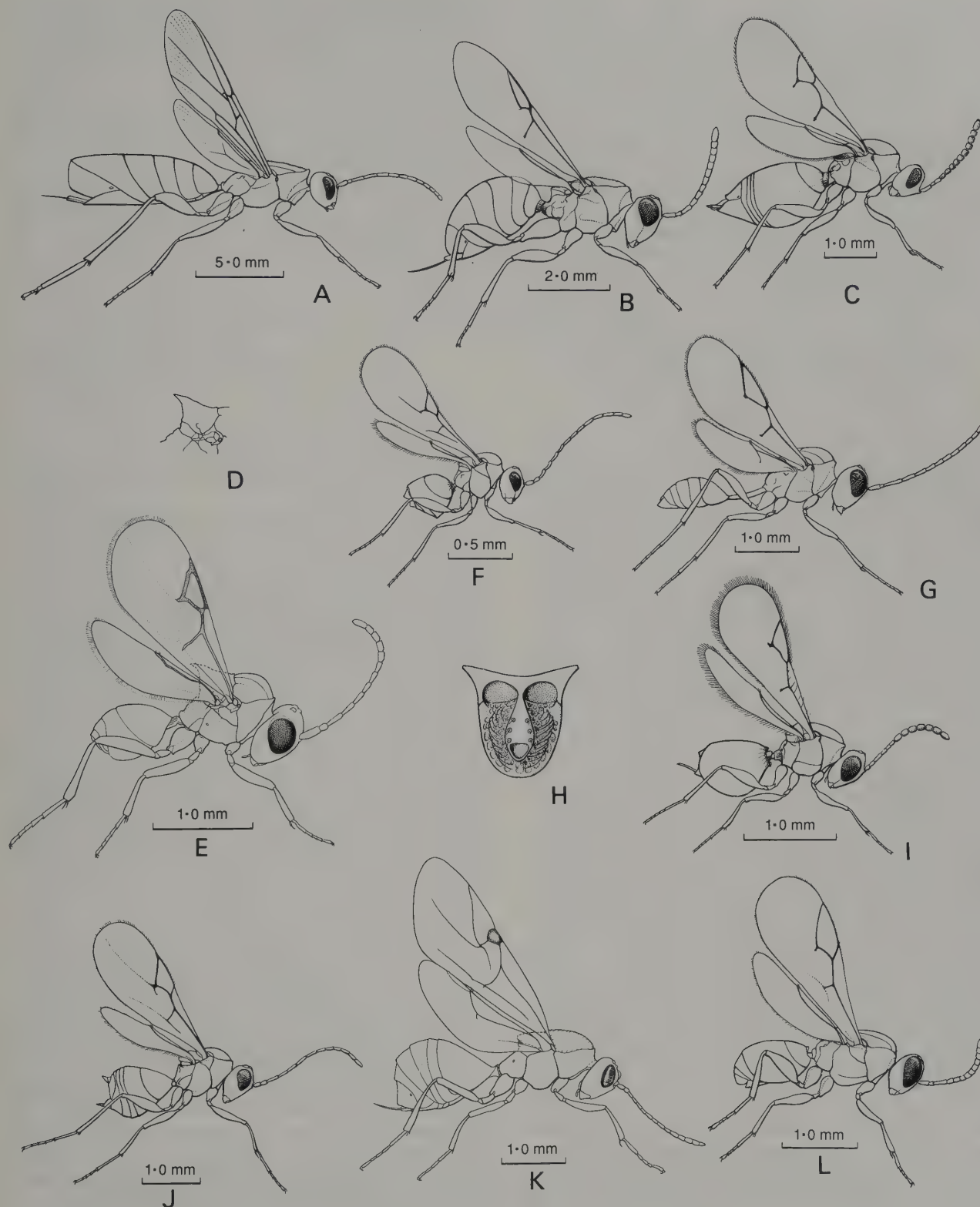


Fig. 42.24 Cynipoidea: A, *Ibalia* sp., Ibaliidae; B, *Mesocynips* sp., Liopteridae-Mesocynipinae; C, *Xyalophora* sp., Figitidae-Figitinae; D, E, *Xyalaspis* sp., Figitidae-Anacharitinae; F, *Alloxysta victrix*, Charipidae; G, *Anacharis* sp., Figitidae-Anacharitinae; H, cup of Eucoilidae; I, *Leptopilina* sp., Eucoilidae; J, *Phanacis hypochoeridis*, Cynipidae-Cynipinae; K, *Austrocynips mirabilis*, Cynipidae-Austrocynipinae; L, *Thrasorus* sp., Cynipidae-Cynipinae.

[A–C, F–J, L by S. Monteith; D, E by T. Nolan; K by A. Hastings]

## Key to the Families of Cynipoidea Known in Australia

1. Radial cell at least 9 times as long as broad (Fig. 42.24A); hind basitarsus almost twice as long as segments 2–5 combined (Fig. 42.7i); T7 the largest gastral tergum ..... **Ibaliidae** (p. 956)  
 Radial cell not 9 times as long as broad; hind basitarsus not twice as long as segments 2–5 combined; T7 not the largest gastral tergum ..... 2
- 2(1). T6 the largest gastral tergum (3 small terga between this and petiole) (Fig. 42.24B) ..... **Liopteridae**-MESOCYNIPINAE (p. 956)  
 T3, T4 or T3 + T4 the largest gastral tergum (never more than one small tergum between this and petiole) (Figs 42.24C, E, F, I–L) ..... 3
- 3(2). Scutellum with raised cup or plate (Fig. 42.24H) ..... **Eucoilidae** (p. 956)  
 Scutellum without raised cup or plate ..... 4
- 4(3). Scutellum, vertex, mesonotum and mesepisternum smooth ..... **Charipidae** (p. 956)  
 Scutellum and usually also vertex, mesonotum and mesepisternum sculptured ..... 5
- 5(4). Scutellum spinose (Figs 42.24D, E) ..... 6  
 Scutellum not spinose ..... 7
- 6(5). 1st gastral tergum (T3) mid-dorsally longer than T4 (Fig. 42.24E) ..... **Figitidae**-ANACHARITINAE (pt, p. 956)  
 1st gastral tergum (T3) mid-dorsally shorter than T4 (Fig. 42.24C) ..... **Figitidae**-FIGITINAE (p. 956)
- 7(5). Petiole longer than wide (Fig. 42.24G) ..... **Figitidae**-ANACHARITINAE (pt, p. 956)  
 Petiole not longer than wide (Figs 42.24J–L) ..... **Cynipidae** (p. 956)

**25. Ibaliidae** (Fig. 42.24A). These are the largest cynipoids, reaching 15 mm. Petiole very short; gaster strongly laterally compressed; 2nd hind tarsal segment with a truncate process (Fig. 42.7i). Represented in Australia by *Ibalia* (2 introduced spp.) endoparasitic on *Sirex noctilio*. *Ibalia* females are attracted by symbiotic fungi in the oviposition shafts of siricids and oviposit on host eggs or early instar larvae. [Kerrich 1973; Kierych 1973; K. L. Taylor 1981]

**26. Liopteridae** (Fig. 42.24B). MESOCYNIPINAE presumably parasitise larvae of Cerambycidae in wood. *Mesocynips* (2 spp.; 5–9 mm), with a coarsely sculptured mesoscutum, is the only Australian genus. Oberthuerellinae and Liopterinae are restricted to the Afrotropical and Neotropical regions respectively.

**27. Figitidae**. FIGITINAE parasitise immature Diptera, especially Muscoidea, in dung or carrion. *Xyalophora* (1 sp.; Fig. 42.24C) has a prominent scutellar spine and small T3. ANACHARITINAE parasitise immature Hemerobiidae (NEUR). *Anacharis* (1 sp.; Fig. 42.24G) is distinguished from all other Australian cynipoids by a very long petiole (New 1982a). *Xyalaspis* (1 sp.; Figs 42.24D, E) has a prominent scutellar spine and large T3 (New 1979). Aspiceratinae, which attack pupae of aphidophagous Syrphidae (DIPT), occur in all zoogeographical regions except Australia. The hosts of the single, Nepalese species of Himalocynipinae are unknown.

**28. Cynipidae**. A large Northern Hemisphere family poorly represented in Australia. Hypopygium produced posteriorly to form a small spine. The AUSTROCYNIPINAE are a monotypic, endemic subfamily. *Austrocynips mirabilis* (Fig. 42.24K), reared from seeds of hoop pine, *Araucaria cunninghamii*, is unique among Cynipoidea in having a pterostigma in the fore wing (Riek 1971a). CYNIPINAE are gall formers or inquilines. *Andricus* (1 sp.) on oaks (*Quercus* spp.) and *Phanacis hypochoeridis* (Fig. 42.24J) in flower stems of dandelion (*Taraxacum officinale*) are introduced. Species of the endemic *Thrasorus* (7 spp.; Fig. 42. 24L) have been reared from stem galls of

Ormocerinae (Pteromalidae) on *Eucalyptus* and *Acacia* where probably they are inquilines. The Pycnostigmatinae are restricted to Africa.

**29. Charipidae** (Fig. 42.24F). Small (less than 2 mm), smooth species. ALLOXYSTINAE, represented in Australia by *Alloxysta* and *Phaenoglyphis*, are common hyperparasites of aphids through Aphidiinae (Braconidae) or Aphelinidae. CHARIPINAE (*Dilyta*) are primary parasites of Psylloidea. [Andrews 1978; Quinlan and Evenhuis 1980]

**30. Eucoilidae** (Figs 42.24H, I). Distinguished from all other cynipoids by having a raised cup or plate on the scutellum. Common in moist forests. Species are endoparasitic and emerge from puparia of cyclorrhaphous Diptera. *Leptopilina bourlardi* is a cosmopolitan parasite of *Drosophila melanogaster*. '*Eucoila*' *occipitalis* parasitises Sarcophagidae. Other Australian eucoilids have been reared from Sphaeroceridae, Muscidae and leaf-mining Agromyzidae. *Cothonaspis*, *Ganaspis*, *Kleidotoma* and *Trybliographa* are common genera. [Weld 1952; Nordlander 1982; Quinlan 1986]

## Superfamily CHALCIDOIDEA

Chalcidoidea develop as parasites or hyperparasites of other insects or arachnids, or as phytophages in galls, seeds or other plant tissue. Adults tend to be small (most are less than 3 mm long, although a few reach 40 mm) and many are metallic in colour.

The superfamily is the largest in the order and there are possibly 100 000 species world-wide (Noyes 1978). The chalcidoid families are a morphologically and biologically diverse assemblage united by a few unique features of the mesosomatic musculature and endoskeleton (Gibson 1986a). Reduced wing venation (Figs 42.25–28), the absence of jugal and anal lobes from the hind wing, the absence of subantennal and median mesoscutal grooves, geniculate 13-segmented antennae, a 1-1-2 tarsal spur formula, loss of spiracles from all metasomal terga except T8, and the loss of the basal ring from the male



genitalia probably also form part of the chalcidoid groundplan. The number of antennal segments is reduced in many families and commonly one or more flagellar segments are modified as anelli. A trochantellus is sometimes visible. The tibial spurs are sometimes inconspicuous and often one of the hind tibial spurs is lost; occasionally the fore tibial spur is absent. The cercus is digitiform or plate-like.

In most chalcidoid larvae the mandibles are triangular, the maxillae and labium are partially or completely fused and the labial palps are not visible. The spinneret is absent and larvae do not form a cocoon (except *Euplectrus* and allied eulophid genera which spin silk from the Malpighian tubules through the anus). First instar larvae are diverse (hymenopteriform, planidial, mymariform, vesiculate, encyrtiform or sacciform) reflecting biology rather than phylogenetic affinity.

The chalcidoid families fall into six, somewhat vaguely defined, and possibly not monophyletic groups.

(1) Families belonging to the mymaromatid group (Mymaromatidae and possibly the Mesozoic Serphitidae) are the only Terebrantia to have a 2-segmented petiole. Possibly they are the sister group to the remaining chalcidoid families.

The remaining families share 3 apomorphies: (i) The mesothoracic spiracle is located at the edge of the mesoscutum, a feature unique within the Hymenoptera. (ii) The prepectus is exposed and separates the pronotum from the tegula. (Secondarily, the prepectus has been lost or fused to the pronotum in a few families and genera and in these the pronotum and tegula are more or less contiguous.) (iii) The multiporous plate sensilla of the female antennae appear to differ ultrastructurally from those of all other Terebrantia (Gibson 1986a).

(2) In the 'chalcidid group' (Chalcididae, Leucospidae, Eurytomidae) the pronotum is mobile and transverse rectangular in dorsal view. Chalcididae and Leucospidae have enlarged, dentate hind femora but such femora occur also in some Torymidae, Agaonidae, Eulophidae and Pteromalidae.

(3) The 'torymid group' comprises the Torymidae, Agaonidae and perhaps also the Ormyridae. Torymids and agaonids are similar in the structure of the posterior of the head (postgenal bridge generally present) and the apex of the metasoma (epipygium free, cerci generally long).

(4) The 'pteromalid group' includes the Pteromalidae, Eucharitidae and Perilampidae. Similarities in the planidial larvae suggest that the Perilampidae and Eucharitidae are closely related to each other, and chrysolampine pteromalids are in several respects (e.g. in their incom-

pletely fused T3 and T4) intermediate between Perilampidae and Pteromalidae.

(5) In the 'encyrtid group' (Eupelmidae, Encyrtidae, Tanaostigmatidae) an inflated mesopleuron and enlargement of the mid leg, its spur and plantar tarsal setae are correlated with enlargement of certain mesosomatic muscles associated with jumping. The inflated mesopleuron (often with complete loss of mesopleural impression and sulci) and leg modifications occur in most female Eupelmidae and all Encyrtidae and Tanaostigmatidae. Less specialised Eupelmidae and in particular male eupelmines resemble cleonymine Pteromalidae.

(6) The 'eulophid group' comprises the Eulophidae, Elasmidae, Aphelinidae, Signiphoridae, Trichogrammatidae, Tetracampidae, the New Zealand Rotoitidae (Bouček and Noyes 1987) and possibly the Mymaridae. Eulophidae and Elasmidae both have advanced axillae, 4-segmented tarsi, and a reduced number of antennal segments. Trichogrammatidae, which also have abbreviated antennae, are the only Chalcidoidea (apart from a few apterous, male Agaonidae) with 3-segmented tarsi. Most chalcidoids have a curved fore tibial spur but this is straight in Eulophidae, Elasmidae and Trichogrammatidae, and is weak in Tetracampidae. The wing venation, the interrupted submarginal vein and the mesoscutellar setae of Tetracampidae recall entedonine Eulophidae. However tetracampids have an occipital carina and a short, straight, bifid fore tibial spur, and are sometimes regarded as being close to the Pteromalidae. Aphelinidae resemble Eulophidae in having complete notauli, advanced axillae and a reduced number of antennal segments, and the enlarged hind coxae of eriaporine aphelinids recall the hind coxae of Elasmidae (which are closely related to Eulophidae). The inflated mesopleuron and large mid tibial spur of some Aphelinidae appear to be a convergence with the condition in the encyrtid group of families. Signiphoridae possibly are most closely related to aphelinids. The Mymaridae are very unusual among the Chalcidoidea by virtue of their peculiar head structure with sulci and usually widely separated antennal sockets. Cephalic sulci of various kinds occur also in some Eulophidae, Trichogrammatidae and Aphelinidae but probably are not homologous with those of mymarids. Family and subfamily keys given below are based on Bouček (1988) who gave keys to the Australian genera of most families and annotated lists of species. Diagnoses and keys in Prinsloo (1980) and Yoshimoto (1984) are also useful. Several of the chalcidoid families accepted in the following pages are regarded as subfamilies by some authors.

#### *Key to the Families of Chalcidoidea Known in Australia*

1. Tarsi 3-segmented, segments elongate and almost of same length; body minute, rarely more than 1 mm long, always non-metallic, never completely smooth, mostly fully winged; postmarginal vein absent (Fig. 42.28A); notauli complete; antennae short, 4–9-segmented (Figs 42.28B, C) ..... **Trichogrammatidae** (p. 969)
- Tarsi 4- or 5-segmented; or, if with fewer segments, then some tarsal segments very short, body yellowish and smooth, wingless, without complete notauli ..... 2
- 2(1). Petiole distinctly 2-segmented and very slender (Fig. 42.25D); fore and hind wings basally narrowed into a linear stalk; mandibles with teeth turned outwards (exodont); antennal sockets closer to eyes than to each other; body minute, less than 1 mm long ..... **Mymaromatidae** (p. 959)

- Petiole, if conspicuous, 1-segmented or, if apparently 2-segmented then all other characters different ..... 3
- 3(2). Macropterous (usually) with hind wing basally very slender (without membrane) (Fig. 42.27I); frons with H-shaped impressed lines; adorbital vertical lines connected not far above antennae by a straight cross-line; antennal sockets much nearer to eyes than to each other; fore wing almost always without postmarginal vein, stigmal vein reduced to a short stub and usually situated well before middle of anterior margin; body usually less than 2 mm long ..... **Mymaridae** (p. 970)
- Not as above ..... 4
- 4(3). Mesothoracic pleuron greatly enlarged, convex, (i.e. without lines, grooves or pits; Figs 42.27C, D, F); prepectus with its posterior margin often loose and thin; spur of mid tibia often large and minutely hairy ..... 5
- Mesopleuron not as above, distinctly subdivided at least by an oblique impression or a line from mid coxa towards fore wing; prepectus posteriorly embedded between and mostly tightly connected with, surrounding sclerites; spur of mid tibia usually thin ..... 8
- 5(4). Prepectus produced anteriorly (Fig. 42.27E) ..... **Tanaostigmatidae** (p. 967)
- Prepectus not produced anteriorly ..... 6
- 6(5). Mesoscutum with complete, groove-like notauli which are widely separated where they reach the axillae (Fig. 42.27K); axillae broadly separated; marginal vein usually very long and then postmarginal vein absent; funicle at most 5-segmented ..... **Aphelinidae** (pt, p. 968)
- Either notauli not groove-like or not wide apart posteriorly; axillae often medially close to each other or contiguous; if marginal vein relatively long then funicle with more than 5 segments ..... 7
- 7(4). Mid coxae much nearer to fore coxae than to hind ones (Fig. 42.27F); mesoscutum convex and short, notauli absent or indicated by superficial lines strongly converging to meet at mesoscutellum (Fig. 42.27G); axillae often contiguous; marginal vein often shorter than the stigmal ..... **Encyrtidae** (p. 967)
- Mid coxae much nearer to hind coxae than to fore ones (Fig. 42.27C); mesoscutum often with notaular depressions; axillae usually widely separated; marginal vein always much longer than stigmal vein ..... **Eupelmidae** (p. 966)
- 8(4). Hind femur strongly enlarged, with ventral teeth (Figs 42.25B, C, G); gaster convex, non-collapsing ..... 9
- Hind femur not strongly enlarged and toothed; in doubtful cases gaster not convex, dorsally collapsing ..... 11
- 9(8). Gena posteriorly with strong carina ..... **Chalcididae** (p. 960)
- Gena posteriorly rounded ..... 10
- 10(9). Fore wing longitudinally folded when at rest; tegula long (Fig. 42.25G); ovipositor curved anterodorsally ..... **Leucospidae** (p. 961)
- Fore wing not longitudinally folded when at rest; tegula short, broad; ovipositor not curved anterodorsally ..... 14
- 11(8). Mesoscutellum in the form of a transverse band (Fig. 42.28D), axillae indistinct; propodeum with a median, triangular area; body usually less than 1 mm long, dorsoventrally flattened, smooth; antennae short, with 2–4 very small funicular segments and long, unsegmented club ..... **Signiphoridae** (p. 968)
- Not as above ..... 12
- 12(11). Hind coxa very large (Fig. 42.28J), disc-like; mid and hind femora flattened; funicle 3-segmented; occipital margin carinate; median portion of metanotum forming flat triangle ..... 13
- Hind coxa smaller, not disc-like; femora, funicle, occipital margin, metanotum usually different ..... 14
- 13(12). Notauli indistinct; tarsi 4-segmented ..... **Elasmidae** (p. 969)
- Notauli complete but fine; tarsi 5-segmented ..... **Aphelinidae** (pt, p. 968)
- 14(12). Apterous or brachypterous ♀♀ only, found in or close to fig syconia (Fig. 42.26C); eyes very small or vestigial, ocelli usually absent; body yellowish to dark brown or black; tibiae short, spiny; tarsal segments often strongly reduced ..... **Agaonidae** (pt, p. 962)
- ♂♂ and ♀♀, brachypterous or macropterous, different also in most other respects; if males with short wings then not associated with figs and tibiae not short and spiny ..... 15
- 15(14). ♀♀ only, associated with figs; mandibles beneath head with appendages bearing transverse laminae or rows of fine teeth (Fig. 42.26E); head more or less prognathous, medially with a broad channel or depression, this rarely reduced to a fine groove above antennae; scape widened, of irregular shape, 3rd antennal segment not anelliform but produced mesodorsally into a stout spine ..... **Agaonidae** (pt, p. 962)
- ♂♂ and ♀♀; mandibular appendages absent; head and antennae not as above ..... 16
- 16(15). Tarsi 4-segmented ..... 17
- At least fore and hind tarsi 5-segmented ..... 20
- 17(16). ♂♂ only; antenna with 6 conspicuous segments between pedicel and club, exceptionally 5; marginal vein at least 4 times as long as stigmal vein; fore wing mostly very densely pilose, including basal third ..... **Tetracampidae** (pt, p. 968)
- ♂♂ and ♀♀; flagellum with fewer segments or marginal vein shorter than above and at least basal third of fore wing more or less bare ..... 18
- 18(17). Stigmal vein fairly long and at very nearly a right angle with the rather short marginal vein (Fig. 42.26B); postmarginal vein strongly reduced; body yellowish and almost smooth, with few setae on thorax; basitarsus fully twice as long as next segment; associated with figs ..... **Agaonidae** (pt, p. 962)
- Either stigmal vein not at a right angle or body not yellow and smooth; basitarsus usually shorter than above ..... 19
- 19(18). Notauli straight, posteriorly further apart than the mesoscutellum is long; body less than 1 mm long ..... **Aphelinidae** (pt, p. 968)



- Notauli not as above; body 0.5–6.0 mm long ..... **Eulophidae** (p. 968)
- 20(16). Notauli complete, very widely separated (Fig. 42.27K); gaster broadly sessile; postmarginal vein usually absent; body usually less than 1 mm long; non-metallic ..... **Aphelinidae** (pt, p. 968)
- Notauli, if complete, not so widely separated; gaster often distinctly separated from mesosoma; postmarginal vein usually developed; body usually larger, often metallic ..... 21
- 21(20). Pronotum subrectangular, large (Fig. 42.25A); gaster convex, non-collapsing; ovipositor at most slightly exerted; non-metallic, usually black or marked with yellow or red; lower mesepimeron not separated; mesosoma usually coarsely punctate ..... **Eurytomidae** (p. 961)
- Pronotum usually different but, if subrectangular then either gaster collapsing or body partially metallic or mesosoma not coarsely punctate; lower mesepimeron often delimited by a groove ..... 22
- 22(21). Occipital carina present and marginal vein at least 5 times as long as narrow, pedunculate part of stigmal vein (Figs 42.25E, F, 26A); antenna 13-segmented; hind coxa either greatly enlarged (Figs 42.25E, 26A) or fore wing with distinctly knobbed stigma (Fig. 42.25F); ovipositor often distinctly exerted, often long; notauli complete, posteriorly subparallel ..... 23
- Occipital carina often absent or, if present then either marginal vein not so much longer than the pedunculate part of stigmal vein, or antenna with fewer than 13 segments; if ovipositor exerted then notauli incomplete or antenna 12-segmented ..... 24
- 23(22). Gaster with transverse rows of large, deep punctures and ridges (Fig. 42.26A); ovipositor not usually exerted ..... **Ormyridae** (p. 962)
- Gaster without such rows (Figs 42.25E, F); ovipositor usually exerted ..... **Torymidae** (p. 962)
- 24(22). Axillae contiguous, although sometimes only narrowly so; pronotum usually not visible from above, often fused with prepectus (Fig. 42.27B); labrum digitate, with radiating rows of lanceolate setae (often concealed by clypeus) ..... **Eucharitidae** (pt, p. 965)
- If axillae contiguous, pronotum visible from above; prepectus usually free; labrum not as above ..... 25
- 25(24). ♀♀ only; antenna with 6 distinct funicular segments and sometimes with 1 anellus; fore wing mostly with dense pubescence reaching the base, very long marginal vein and short stigmal vein; notauli deep, complete; propodeum often extensively pubescent ..... **Tetracampidae** (pt, p. 968)
- ♂♂ and ♀♀; antenna usually different but, if similar to above then pubescence of fore wing reduced in basal third and venation different; notauli often incomplete; propodeum almost always without pubescence mesad of spiracles ..... 26
- 26(25). Prepectus often fused with lateral panel of pronotum (Fig. 42.27A); if prepectus clearly separated then face with distinct supraclypeal area and mandibles strong, bidentate; notauli complete; 1st and 2nd gastral terga (T3 and T4) partially fused, at least dorsally, although suture still visible ..... **Perilampidae** (p. 965)
- Prepectus usually clearly separated from pronotum and if supraclypeal area distinct then mandibles not as above; gastral terga not as above ..... 27
- 27(26). ♀♀; gaster with protruding narrow tail (Fig. 42.26D) which is formed either by ovipositor alone (with sheaths) or by ovipositor covered by narrowly extended terminal terga ..... 28
- ♂♂ and ♀♀; gaster without such tail ..... 29
- 28(27). Apex of tail curving downwards (Fig. 42.26D), not flanged like a dart's tail; notauli complete and antenna 12-segmented, with 1–3 anelli; associated with figs ..... **Agaonidae** (pt, p. 962)
- Tail not curving downwards; either notauli incomplete or antenna with 13 segments or antenna with 12 segments and tail dart-like or antenna with fewer than 12 segments ..... **Pteromalidae** (pt, p. 963)
- 29(27). Mandibles sickle-shaped, slender; lower face either with well-defined supraclypeal area or with very deep tentorial pits; marginal vein of fore wing unusually long but apex of venation often ill-defined, with stigmal vein always very short (Fig. 42.27B), almost perpendicular ..... **Eucharitidae** (pt, p. 965)
- Mandibles not sickle-shaped, broader; if supraclypeal area distinct or tentorial pits deep then fore wing with much shorter marginal vein and oblique stigmal vein longer than above ..... 30
- 30(29). ♀♀ only; insertion of hind coxa well above that of mid coxa (Fig. 42.26B); mesosoma dorsally with fine, dense punctation or smooth; apex of gaster usually curving downwards; associated with figs ..... **Agaonidae** (pt, p. 962)
- ♂♂ and ♀♀; insertion of hind coxa not well above that of mid coxa (Fig. 42.26J); mesosoma dorsally not as above, often reticulate; apex of gaster of ♀♀ not curving downwards; rarely associated with figs ..... **Pteromalidae** (pt, p. 963)

**31. Mymarommatidae** (Fig. 42.25D). Minute, 0.4–0.9 mm; not strongly sclerotised, finely sculptured, non-metallic; gena not posteriorly carinate; antennal sockets much closer to each other than to compound eyes; vertex and frons without the specialised sulci present in Mymaridae; occipital surface separated from rest of head by transverse, membranous, often pleated band; mandibles exodont; antennae 9–11-segmented and clubbed in females, 13-segmented and filiform in males;

pronotum not conspicuous in dorsal view; prepectus concealed beneath lateral panel of pronotum; notauli absent; axillae not advanced; mesopleuron not enlarged; fore wing stalked, with long marginal cilia, surface reticulate, without hypochaeta; fore wing venation reduced to a single, short vein not extending beyond stalk; hind wing reduced to a minute, apically bifurcate stalk which clasps the fore wing; legs slender; tarsi 5-segmented; fore tarsus without strigil comb; petiole 2-segmented (comprising

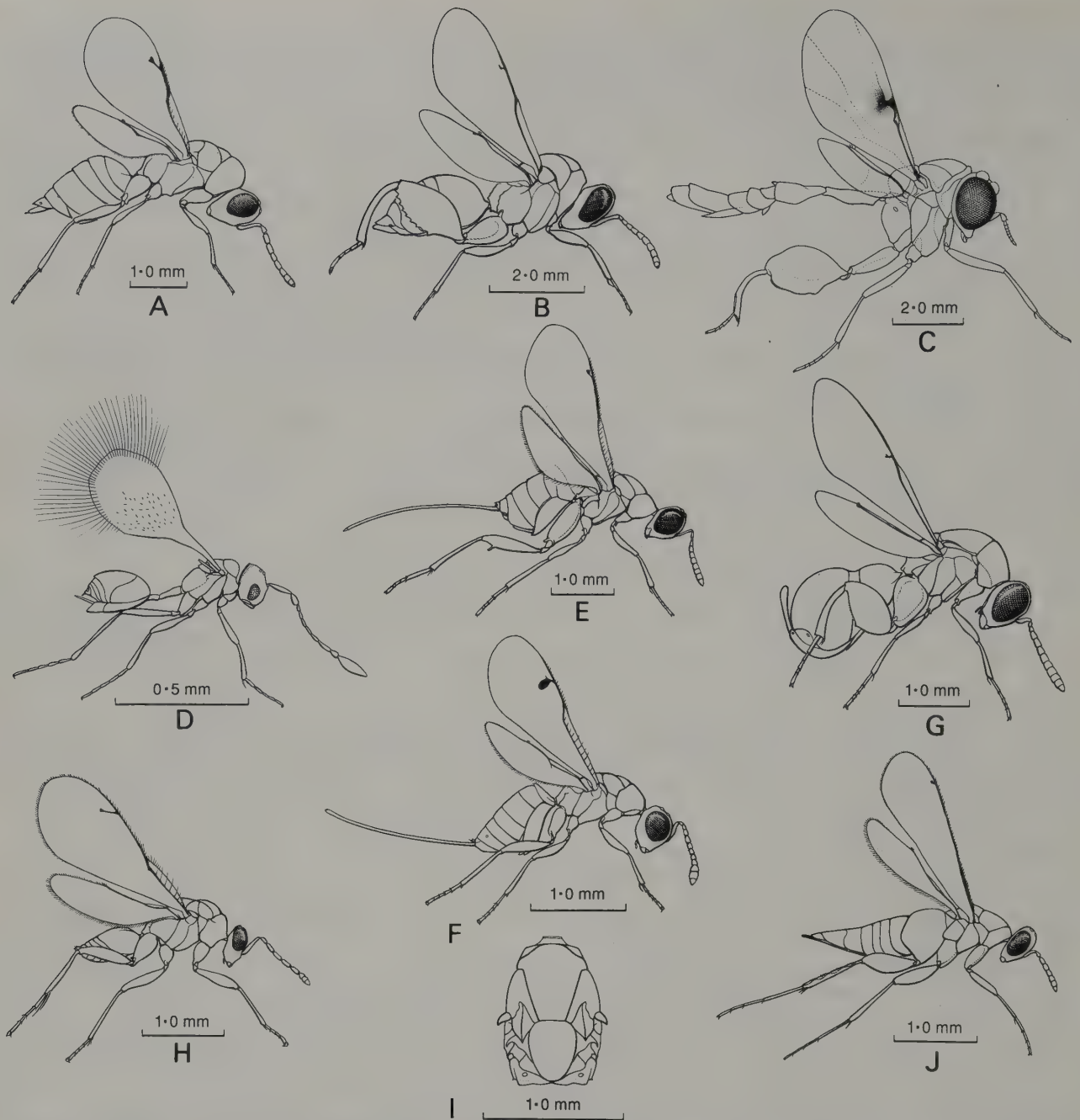


Fig. 42.25 Chalcidoidea: A, *Eurytoma* sp., Eurytomidae-Eurytominae; B, *Brachymeria* sp., Chalcididae-Chalcidinae; C, *Smicromorpha doddi*, Chalcididae-Smicromorphinae; D, *Palaeomymar* sp., Mymarommatidae; E, *Diomorus* sp., Torymidae-Toryminae; F, *Megastigmus* sp., Torymidae-Megastigminae; G, *Leucospis giraulti*, Leucospidae; H, *Euplectrus* sp., Eulophidae-Eulophinae; I, *Euderus* sp., Eulophidae-Euderinae, mesosoma, dorsal; J, *Elasmus* sp., Elasmidae.  
[A, B, E–H, J by S. Monteith; C, I by T. Nolan; D by A. Hastings]

abdominal segments 2 and 3); cerci not advanced; ovi-positor not exerted.

The bellows-like band in the head apparently enables the head to expand or contract like an accordion. The biology of mymarommatids is unknown, but probably they are egg parasites. Australian species occur in moist forest regions. [Gibson 1986a; Huber 1986]

**32. Chalcididae** (Figs 42.25B, c). Body 1.5–16 mm; strongly sclerotised; head, mesosoma and sometimes

metasoma strongly punctate; dark, pale or brightly coloured, rarely metallic; gena posteriorly with sharp carina; fore wings not longitudinally folded; hind femur enlarged, ventral margin dentate; tarsi 5-segmented.

Chalcididae are usually solitary endoparasites of mature larvae or pupae of Lepidoptera, although Diptera, Neuroptera, Hymenoptera and Strepsiptera are also recorded as hosts. Some species are facultative or obligate hyperparasites via Tachinidae, Ichneumonidae or Bracon-



idae. Some primitive genera (in the Phasganophorini and the extralimital Cratocentrini) parasitise immature stages of Coleoptera in wood.

Most genera occurring in Australia are also represented in New Guinea or the Oriental, Afrotropical or Palaearctic regions. Few genera are endemic.

#### Key to the Subfamilies of Chalcididae

1. Hind tibia apically tapering to a strong spine, extending far beyond insertion of basitarsus; with only 1 spur between basitarsus and tip of spine, this spur often inconspicuous ..... 2  
Hind tibia truncate, rarely forming a short spine; with 2 spurs ..... HALTICHELLINAE
- 2(1). Metasoma slender, attached high on propodeum, remote from hind coxae (Fig. 42.25c) ..... SMICROMORPHINAE  
Metasoma not slender, attached to propodeum near hind coxae ..... 3
- 3(2). Head with prominent, carinate horns between antennal scrobes and compound eyes ..... DIRHININAE  
Head without such horns ..... 4
- 4(3). Petiole narrow, without longitudinal ridges, more than half as long as gaster; postmarginal vein absent ..... EPITRANINAE  
Petiole usually very short and concealed from above; if petiole longer than wide then postmarginal vein present ..... CHALCIDINAE

**HALTICHELLINAE.** In Haltichellini the marginal vein of the fore wing lies along the margin and the postmarginal vein is absent. Most Australian species belong to *Antrocephalus* (80 spp.) which is distributed widely in the Palaearctic, Afrotropical and Oriental regions; Lepidoptera are common hosts. Females of the endemic *Trichoxenia* (1 sp.) sometimes reach 14 mm in length and have a spinose mesoscutellum. The mesoscutellum is mound-like in the Indo-Australian *Uga* (1 sp.), species of which parasitise Coccinellidae.

In Hybothoracini the marginal vein of the fore wing is removed slightly from the margin and the postmarginal vein is absent. *Proconura* (7 spp.) is widespread from southern Europe to Australia and the Pacific islands; Australian species have been reared from Pyralidae, Gelechiidae and Tortricidae. *Irichohalticella* (9 spp.) is restricted to Australia and New Guinea and parasitises Oecophoridae.

Tropimeridini (*Tropimeris*; 1 sp.) differ from Hybothoracini in having the toruli remote from the oral margin.

EPITRANINAE parasitise Pyralidae and Tineidae (LEPI). *Epitranus* (6 spp.) also occurs in the Afrotropical and Oriental regions.

DIRHININAE are reared from puparia of Calliphoridae, Sarcophagidae, Muscidae and Tephritidae (DIPT). *Dirhinus* (8 spp.) is widespread in warmer parts of the Afrotropical, Palaearctic, Oriental, Australian and Pacific regions.

CHALCIDINAE. Of the 4 recognised tribes only the Cratocentrini are absent from Australia. Phasganophorini parasitise immature stages of Coleoptera in wood. The metasoma is elongated posteriorly in *Megalocolus* (10

spp.). *Trigonura euthyrrhini* parasitises Curculionidae in mango seeds.

Brachymeriini include only *Brachymeria* (70 spp.; Fig. 42.25B), which is diverse and common throughout the warmer parts of the world. Australian species have been reared from pupae of Lepidoptera, Chrysomelidae (COLE) and Pergidae and from puparia of Tachinidae and various synanthropic Diptera. Some extralimital species have very wide host ranges (e.g. *Brachymeria ovata* has been reared from pupae of 22 species of Lepidoptera and from Braconidae, Ichneumonidae and Tachinidae parasitising Lepidoptera). Chalcidini (*Chalcis*; 1 sp.) are most diverse in Central and South America. Extralimital species oviposit into the eggs of Stratiomyidae (DIPT) and emerge from puparia.

SMICROMORPHINAE (Fig. 42.25c) parasitise the immature stages of *Oecophylla* (Formicidae) in tropical areas (Naumann 1986). Adults usually are pale coloured, with large eyes and ocelli, and sometimes are attracted to light. *Smicromorpha* (5 spp.) also occurs in the Afrotropical and Oriental regions. [Bouček 1988]

**33. Leucospidae** (Fig. 42.25G). Body 5–13 mm; heavily sclerotised; dark with red or yellow markings, sometimes metallic; gena not posteriorly carinate; head, mesosoma and metasoma strongly punctate; tegula very elongate, anteriorly almost reaching posterior margin of pronotum; fore wings longitudinally folded when at rest; hind femur enlarged, ventral margin dentate; tarsi 5-segmented; metasoma strongly sclerotised; T4 mostly concealed by T3, reduced to 2 small, sclerotised lateral panels connected medially by membrane; ovipositor sheaths often (all Australian species) long and curved anterodorsally, and metasoma dorsally with median, ovipositor furrow; metasomal terga of males fused to form carapace.

Leucospidae develop as solitary ectoparasites of larvae of solitary bees (especially Megachilidae), Eumeninae and Sphecidae. The female leucospid oviposits through the wall of the host's aerial nest. Adults are found on flowers or near host nesting sites. In colour and shape many mimic particular aculeates, although it is not necessarily the host species which is the model.

Leucospids are diverse in all tropical and warm temperate regions. *Leucospis* (11 spp.) occurs world-wide and Australian species have been reared from resinous nests of *Megachile* (Megachilidae) and mud nests of *Pison* (Sphecidae). [Bouček 1974, 1988]

**34. Eurytomidae** (Fig. 42.25A). Body 1.0–7 mm; strongly sclerotised; head and mesosoma coarsely punctate; non-metallic (except in a few extralimital species), predominantly dark coloured; gena posteriorly sometimes with sharp carina; pronotum, in dorsal view, broad and more or less rectangular; hind femur generally slender, without teeth; tarsi 5-segmented.

Eurytomidae include parasitic, hyperparasitic and phytophagous species. Those developing in galls of other insects sometimes feed on both the gall-forming insect and the gall tissue.

Heimbrinae, which have unusual metasomal morphology, are restricted to the New World region (Stage and Snelling 1986).



The antennae are 13-segmented (including 2 or 3 anelli) in RILEYINAE (4 spp.), which are predominantly Neotropical. An Australian *Rileyia* (1 sp.) has been reared from cecidomyiid galls (DIPT) on *Santalum lanceolatum* but extralimital genera include species parasitic in eggs of Gryllidae (ORTH) and Cicadidae (HEMI).

In EURYTOMINAE (146 spp.) the antennae are 12-segmented (with 1 anellus). Most *Bruchophagus* (42 spp.) are phytophagous. *B. rodii* is a pest developing in lucerne seed. *B. fellis* causes stem galls on *Citrus*. Other Australian *Bruchophagus* have been reared from *Acacia* seeds and galls on *Eucalyptus* (including galls formed by psyllids, apiomorph eriococcids (HEMI) and ormerocerine pteromalids). Some *Eurytoma* (70 spp.) are phytophagous in seeds but most are parasitic; Australian species have been reared from galls on *Eucalyptus*, *Acacia* and *Casuarina*, from various Lepidoptera (Psychidae, Gracillariidae, Tortricidae, Limacodidae), from Agromyzidae (DIPT) in stems, from ichneumonid and braconid cocoons, and from the egg sacs of *Latrodectus* (Araneae). *Tetramesa* (3 spp.) is phytophagous in grass seeds or internodes; some extralimital species are pests of cereals. All *Sycophila* (10 spp.) are associated with soft galls and figs, possibly as inquiline. [Bouček 1988]

**35. Torymidae** (Figs 42.25E, F). Body 0.9–30 mm; dark or pale, often brightly coloured, often metallic; generally not strongly sclerotised, not strongly punctate; head with dorsally complete occipital carina (except in some extralimital genera) and closed, postgenal bridge; gena not posteriorly carinate; antennae 13-segmented; fore wings not longitudinally folded; hind femur sometimes enlarged and dentate; T9 and T10 reduced, not fused; epipygium represented by small, median flap; cerci relatively long.

Most torymids are associated with plant galls or seeds, either as gall-formers, as inquilines or as parasites of gall-forming insects. Others are parasitic on insect eggs, immature stages of Lepidoptera or Hymenoptera, or hyperparasitic via Tachinidae (DIPT). Only the Thaumatomyinae (Bouček 1978) are not represented in Australia.

#### Key to the Subfamilies of Torymidae Known in Australia

1. Groove between mesopleuron and metapleuron strongly sinuate (Fig. 42.25E) ..... TORYMINAE
- Groove between mesopleuron and metapleuron straight (Fig. 42.25F) or very slightly curved ..... 2
- 2(1). Stigmal vein longer than breadth of costal cell, with large, apical knob (Fig. 42.25F) ..... MEGASTIGMINAE
- Stigmal vein shorter than breadth of costal cell, with at most a weak, apical knob ..... MONODONTOMERINAE

MEGASTIGMINAE (86 spp.; Fig. 42.25F) are commonly yellow to brown, sometimes with metallic patches. Usually the pronotum is transversely striate and the ovipositor strongly exerted and curved dorsally. Species are associated with galls, as gall-formers, inquilines or parasites. *Megastigmus* (50 spp.) is cosmopolitan; Australian species have been reared (often in association

with pteromalids, coccoids or Diptera) from stem, leaf and flower galls on a variety of plants (*Eucalyptus*, *Brachychiton*, *Hakea*, *Acacia*, *Banksia*, *Citrus*, *Helichrysum*). There are several small, endemic genera, including *Xenostigmus* (3 spp.), species of which cause galls on *Hakea* buds. *Bootanellus orientalis*, which develops in seeds of *Casuarina*, has been introduced accidentally from Australia to India, Hawaii and Cuba, along with the host plant. Large *Bootania* (1 sp.; females up to 30 mm) are phytophagous in seeds of *Pandanus* and widespread in the Western Pacific and Oriental regions.

MONODONTOMERINAE (60 spp.) are mostly metallic with a straight, usually strongly exerted ovipositor.

Australian Monodontomerini have a slender hind femur with at most 1 small tooth. *Torymoides* (17 spp.) is cosmopolitan but most diverse in Australia; most species are parasitic in dipterous galls on herbaceous plants or in the softer parts of woody plants. *Amoturoides breviscapus* is hyperparasitic on tachinid or ichneumonid parasites of *Ropalidia* (Vespidae). There are several small, endemic genera.

Podagrionini resemble Chalcididae in that the hind femur is enlarged and dentate. All parasitise mantid oothecae. *Podagrion* (17 spp.) and *Pachytomoides* (7 spp.) are widespread throughout the warmer regions of the world.

Generally metallic with a strongly exerted ovipositor, TORYMINAE (Fig. 42.25E) are more numerous in the Northern Hemisphere. The hind femur is dentate in a few genera. *Torymus* (3 spp.) is predominantly Holarctic where species are either phytophagous or parasitic in galls; 2 introduced species in Australia develop in seeds of *Sorbus*, *Crataegus* or apples. The petiole is long in *Odopoeia* (2 spp.) and the endemic *Ovidia* (1 sp.). [Bouček 1988]

**36. Ormyridae** (Fig. 42.26A). Body 1–3 mm; occipital carina complete dorsally; heavily sclerotised, predominantly metallic green to blue; gena not posteriorly carinate; fore wings not longitudinally folded; stigmal and postmarginal veins short relative to marginal vein; hind femur slender; tarsi 5-segmented; gaster heavily sculptured with transverse rows of pits and ridges; T8 and T9 relatively elongate, not fused; T10 not present as a separate sclerite; ovipositor not strongly exerted; cerci relatively short.

This small family (about 35 spp. world-wide), containing only the genus *Ormyrus*, is represented on all continents. Australian species develop in the galls of other insects on *Eremocitrus*, *Casuarina* and *Apophyllum*, and in figs. [Bouček 1988]

**37. Agaonidae** (Figs 42.26B–E). Body 1.0–10 mm; pale or dark coloured, commonly metallic; generally weakly sclerotised, without heavy sculpturing; often flattened or collapsing after death; postgenal bridge complete; occipital carina absent (except in a few Epichrysomallinae in which the ovipositor is concealed); antennae variable, sometimes with fewer than 13 segments; fore wings not longitudinally folded; legs slender or slightly expanded in females (Fig. 42.7j) and some males, very stout and spiny in wing-reduced males; tarsi



4- or 5-segmented; T8 and T9 not reduced, sometimes elongate; T10 often represented by median flap; ovipositor either strongly exerted or concealed; cerci usually relatively long.

Sexual dimorphism is usually pronounced and brachypterous or apterous males (Fig. 42.26C) occur in most subfamilies. Wing-reduced males tend to be yellow, with small eyes, stout and spiny fore and hind legs and reduced mid legs.

Agaonids all develop within the figs (syconia) of various species of *Ficus*. To lay their eggs female wasps either oviposit through the wall of the developing fig or enter the fig via the ostiole. Species ovipositing through the fig wall have short or long ovipositors depending on the size of the fig and the thickness of its wall. The effective length of the ovipositor is increased by telescopic elongation of the gaster in some species. Agaonids entering figs to oviposit have shorter ovipositors but are otherwise specialised to force their way through the narrow ostiole (e.g. with smooth, flexible bodies, mandibular appendages or wings which are readily torn away).

Agaonid larvae feed on developing *Ficus* ovules; some (e.g. Agaoninae) promote galls. Larvae of other agaonid subfamilies commonly occur in the same figs as larvae of Agaoninae. The non-agaonine larvae probably compete with the agaonine larvae for food and space but are not parasitic on them. Adults of Agaoninae pollinate the host *Ficus* and the relationship between wasp and plant (blastophagy) is closely symbiotic. Adults of the non-agaonine subfamilies are not pollinators. Agaonines are highly host-specific, each species being restricted to one species of *Ficus* but species of the non-pollinating subfamilies may not be so rigidly host specific. Some species of *Ficus* support several species of Agaonidae and occasionally more than one pollinating species (Ramírez 1974; Bouček *et al.* 1981). Wing-reduced agaonid males usually mate and die without leaving the fig.

Agaonidae are restricted to warmer regions of the world and in Australia are most numerous in tropical regions where *Ficus* are diverse. The life histories of few Australian species are known.

EPICHRYSOMALLINAE (Fig. 42.26B) are non-metallic, yellow to black, lack an exerted ovipositor, and are superficially eurytomid- or pteromalid-like. They are the most primitive agaonids. Females oviposit from outside the fig and the developing larva induces a gall. Frequently they occur in figs in which no agaonines are present. OTITESSELLINAE possibly develop similarly.

In SYCORYCTINAE (Figs 42.26C, D) the strongly exerted ovipositor is sometimes completely covered by an extremely elongate, apical, metasomal tergum. The mesoscutellum lacks lateral grooves. Females oviposit from outside the fig. *Philotrypesis*, *Sycoscapter* and *Apocrypta* occur in Australia.

Sycoecinae occur in the Afrotropical and Oriental regions and reach New Guinea.

The ovipositor of SYCOPHAGINAE is exerted but the apical metasomal tergum is not as long as in Sycoryctinae and the mesoscutellum has lateral grooves. The subfamily is probably the sister group to the Agaoninae. Most

species oviposit from outside the fig. *Pseudidarnes*, *Eukoebelea* and *Apocryptophagus* each have a few Australian species.

AGAONINAE (Fig. 42.26E) are morphologically and biologically the most specialised agaonids. The mandibles of females have appendages bearing ridges or teeth which assist females to force their way through the ostiole of the figs. Within the fig in which they have developed, freshly emerged females actively or passively gather pollen which is carried in specialised folds, pockets or groups of hairs or within the digestive tract. Females leave the fig in search of other figs of the same host species. On locating such a fig, they enter it via the ostiole, pollinate and oviposit. *Pleistodontes* (10 spp.) and *Ceratosolen* are the most frequently encountered Australian agaonines. [Wiebes 1982; Bouček 1988]

**38. Pteromalidae** (Figs 42.26F–J). Body 0.6–40 mm; dark or pale coloured, often metallic; strongly or weakly sclerotised, sometimes strongly sculptured; head usually without a dorsally complete occipital carina; closed, post-genal bridge usually absent, secondarily present in some prognathous genera; gena generally not carinate posteriorly; fore wings not longitudinally folded; hind femur sometimes enlarged, occasionally dentate; T8 and T9 of varied form; T10 sometimes present; cerci usually relatively short. Micropterous or apterous forms occur in a few subfamilies.

This is the most morphologically and biologically diverse chalcidoid family. It is the most difficult to diagnose and males, in particular, commonly are confused with those of Torymidae and Eupelmidae. The family includes parasites and hyperparasites of the eggs, larvae, pupae and (rarely) adults of many orders of insects. Some pteromalid larvae attacking stationary, clustered insects such as coccoids (HEMI) behave more as predators than as parasites. Other pteromalids are phytophagous, either as gall-formers or asinquilines in galls. The more morphologically plesiomorphic pteromalid genera tend to be parasites of Coleoptera in wood or phytophagous.

In Australia 27 subfamilies are represented. Only the Ceinae, Philomidinae, Neodiparinae and Crataminae are absent. Bouček (1988) provided keys to Australian subfamilies and genera.

Generally large and brightly metallic, CLEONYMINAE (60 spp.) commonly are attracted to smooth, sunlit tree trunks. *Agamerion* (15 spp.; Fig. 42.26F) in which the hind femur is enlarged, parasitises cockroach oothecae under bark. Most cleonymines parasitise immature stages of Coleoptera in wood. Some *Thaumasura* (20 spp.) with strongly exerted ovipositors reach 40 mm in length. Rasp-like protuberances on the head of *Marxiana* (1 sp.) are similar to those of *Eusandalum* (Eupelmidae) and Orussidae.

LEPTOFOENINAE are large (up to 25 mm), slender, stephanid-like and parasitise larvae of Coleoptera in wood. The subfamily occurs in Australia (*Doddifoenus*, 1 sp.), New Guinea and the warmer parts of the New World.

MACROMESINAE (cosmopolitan parasites of Scolytinae) and LOURICIINAE (parasites of eggs of Cerambycidae

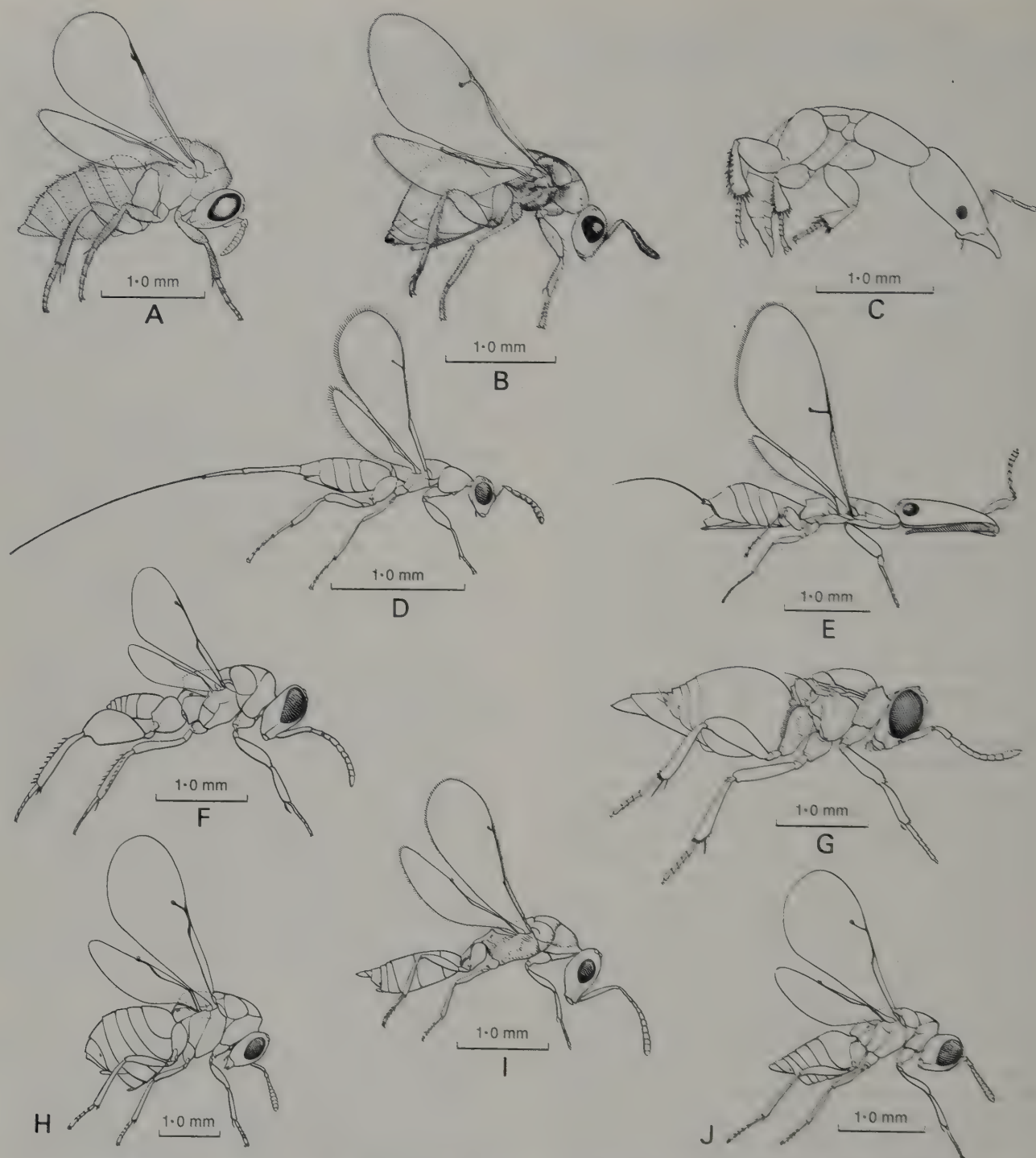


Fig. 42.26 Chalcidoidea: A, *Ormyrus* sp., Ormyridae; B, *Herodotia subatriventris*, Agaonidae-Epichrysomallinae; C, *Sycoscapter australis*, Agaonidae-Sycoryctinae, ♂; D, *Philotrypesis* sp., Agaonidae-Sycoryctinae, ♀; E, *Pleistodontes* sp., Agaonidae-Agaoninae, ♀; F, *Agamerion* sp., Pteromalidae-Cleonyminae; G, *Neapterolelaps* sp., Pteromalidae-Diparinae, ♀; H, *Trichilogaster* sp., Pteromalidae-Ormocerinae; I, *Spalangia* sp., Pteromalidae-Spalangiinae; J, *Nasonia vitripennis*, Pteromalidae-Pteromalinae.  
[A, C, G by T. Nolan; B, D-F, H-J by S. Monteith]

throughout the Old World tropics) are each represented by a single Australian species.

COLOTRECHNINAE (12 spp.) include the cosmopolitan *Colotrechnus* (species parasitic on weevil or dipterous larvae in seed pods) and several genera associated with galls on *Eucalyptus* and *Casuarina*. *Cameronella* (6 spp.)

is endemic and species have been reared from galls of *Apiomorpha* (HEMI: Eriococcidae); the gaster of females has 3 apical flanges like the tail fins of a dart.

DITROPINOTELLINAE are associated with galls on *Acacia*, *Casuarina* and *Eucalyptus*. *Ditropinotella* (5 spp.), the only genus, also occurs in New Guinea.



All ORMOCERINAE (80 spp.) are associated with galls, especially on various Myrtaceae, *Casuarina*, *Acacia* and Poaceae, where they most probably are phytophagous. The subfamily is most diverse in the Australian region where there are 28, mostly endemic, genera. *Trichilogaster* (10 spp.; Fig. 42.26H) forms stem and flower galls on *Acacia*. *Brachyscelidiphaga* (3 spp.) is either an inquiline or a parasite in galls of *Apiomorpha*. *Systasis* is associated with grass seeds.

COELOCYBINAE (30 spp.) are also associated with galls on trees, where at least some are parasitic. The subfamily is represented in Australia (13 genera including *Coelocyba* and *Ormyromorpha*), New Zealand (2 genera) and South America (one genus associated with *Nothofagus*).

Females of DIPARINAE (40 spp.) are often brachypterous, micropterous (Fig. 42.26G) or apterous and are common in the leaf litter of moist forests. An extralimital species parasitises a curculionid larva in subterranean parts of *Cyperus* (Cyperaceae).

Most CEROCEPHALINAE (14 spp.) parasitise wood-boring larvae of Coleoptera (especially Scolytinae, Anobiidae, Bostrichidae). *Theocolax elegans* is a cosmopolitan parasite of Coleoptera in stored grain.

Black, flattened SPALANGIINAE (10 spp.) attack dipterous puparia. The 2 most common, Australian species of *Spalangia* (Fig. 42.26I) are cosmopolitan parasites of Calliphoridae, Sarcophagidae and Muscidae associated with dung and carrion.

ASAPHINAE (8 spp.) include *Asaphes vulgaris*, an introduced hyperparasite on aphids, and the endemic *Enoggera* (5 spp.), a parasite of eggs of paropsine Chrysomelidae (COLE).

PARASAPHODINAE (*Parasaphodes*, 1 sp.) and AUSTROTEROBIINAE (*Austroterobia*, 1 sp.) parasitise coccoids (HEMI), especially species of *Icerya* (Margarodidae). HERBERTIINAE (*Herbertia*, 2 spp.) attack leaf-mining Agromyzidae (DIPT). EROTOLEPSIINAE (1 sp.) also occur in the Neotropical region.

EUNOTINAE (40 spp.; 11 genera) are particularly diverse in Australia. Their larvae are parasites, hyperparasites or predators on coccoids and psyllids (HEMI). Species of *Moranila* (10 spp.) and *Ophelosia* (4 spp.) have been introduced from Australia to other countries for the biological control of scale insects.

*Collessina* (1 sp.; EUTRICHOSOMATINAE), known only from Qld, may not be related closely to the New World eutrichosomatine genera.

The PTEROMALINAE (150 spp.) include parasites of Lepidoptera (e.g. *Pteromalus*, *Dibrachys*), leaf-feeding or wood-boring Coleoptera (e.g. *Epanogmus*), puparia of synanthropic Diptera (e.g. *Nasonia*, Fig. 42.26J), aphids or aphidophagous Syrphidae (*Pachyneuron*). Some (e.g. *Dinarmus*) attack Coleoptera in seeds. *Lariophagus* and *Anisopteromalus* include cosmopolitan parasites of Coleoptera in stored grain. Some Pteromalinae are hyperparasitic and a few are associated with plant galls.

MISCOGASTERINAE (3 spp.) are predominantly Holarctic with only a few Neotropical, Oriental and Australian genera. All parasitise larvae of Diptera in leaf mines or stem tunnels.

*Panstenon* (5 spp.; PANSTENONINAE) is cosmopolitan and parasitises insect eggs and larvae in grass stems.

Apart from an undescribed Oriental genus CHROMEURYTOMINAE (15 spp.) are restricted to Australia. Species are torymid-like with an occipital carina and strongly exerted ovipositor. *Chromeurytoma* (14 spp.) is associated with galls on *Eucalyptus* and *Acacia*. *Asaphoideus* (1 sp.) has been reared from a leaf-miner in citrus.

PIRENINAE (20 spp.) parasitise Cecidomyiidae (DIPT) in plant tissues.

NEFOENINAE (2 spp.), STOREYINAE (1 sp.), KEIRANINAE (1 sp.) and AUSTROSYSTASINAE (1 sp.) are all small, endemic subfamilies. Austrosystasinae are associated with galls on *Elaeocarpus* and Keiraninae have been reared from a margarodid coccoid (HEMI) but nothing is known biologically of the others. [Bouček 1988]

**39. Perilampidae** (Fig. 42.27A). Body 1.3–4.5 mm; head and mesosoma strongly sclerotised, often strongly sculptured; dark to bright metallic green or blue; gena sometimes posteriorly carinate; antennae 13-segmented, sexually dimorphic (in males scape distally expanded, with pores; funicle stouter); fore wings not longitudinally folded; legs slender; tarsi 5-segmented; T3 and T4 dorsally more or less fused, laterally separated, often giving gaster (in lateral view) a triangular shape with the more posterior segments telescoped within T3 + T4.

In PERILAMPINAE the right mandible is tridentate and the prepectus is fused to the pronotum (except in the extralimital *Steffanolampus*). Species are robust and usually coarsely sculptured. Females oviposit on plants and the 1st instar larva is a mobile planidium. Later instars of *Perilampus* (30 spp.) develop as endoparasites of phytophagous larvae (especially Lepidoptera, Chrysomelidae, Symphyta) or as hyperparasites (via Braconidae, Ichneumonidae or Tachinidae) in these larvae or in acridids. Planidia of *Monacon* (2 spp.) enter platypodine or scolytine tunnels in wood and later instars feed ectoparasitically on pupae of these beetles. Both genera are widespread outside Australia.

CHRY SOLAMPINAE are less robust and not so coarsely sculptured. The right mandible is bidentate and the prepectus is not fused to the pronotum. Extralimital species parasitise immature stages of Coleoptera (Curculionidae, Nitidulidae, Lyctinae); at least one has a planidial 1st instar larva. *Chrysolumpus* (22 spp.) is a cosmopolitan genus. [Bouček 1988]

**40. Eucharitidae** (Fig. 42.27B). Body 1.7–11 mm; head and mesosoma strongly sclerotised, often strongly sculptured; colours diverse, often metallic green or blue; gena not posteriorly carinate; labrum digitate, i.e. with finger-like processes; mandibles large, sickle-shaped (reduced in the extralimital Echthrodapinae); antennae with variable number of segments (fewer than 13 in some Australian species, up to 22 in some extralimital species); head small relative to robust mesosoma; fore wings not longitudinally folded; postmarginal and stigmal veins short relative to marginal vein; legs slender; tarsi 5-segmented; ovipositor generally concealed.

Female eucharitids oviposit on plants. The planidial 1st instar larvae attach themselves to foraging worker ants

and are carried to the ant nest where the planidia transfer themselves to the immature stages of the ants. The planidial larvae burrow into the ant larvae where they and later larval instars develop endoparasitically. Australian species have been associated with species of *Ectatomma*, *Camponotus*, *Pheidole* and *Myrmecia*.

*Key to the Subfamilies of Eucharitidae Known in Australia*

1. Pronotum visible in dorsal view ..... AKAPALINAE
- Pronotum not visible in dorsal view ..... 2
- 2(1). Pronotum and prepectus not fused ..... ORASEMINAE
- Pronotum and prepectus fused ..... EUCHARITINAE

The AKAPALINAE (*Akapala* only; 2 spp.) are endemic and rarely collected. ORASEMINAE (*Orasema* and *Orasemorpha* only) and EUCHARITINAE (12 genera) are more common. The scutellum sometimes bears bizarre processes, e.g. a long spine (*Thoracanthoides*) or fork (*Schizaspidia*). The antennae have only 9 apparent segments in some female *Tricoryna* and are ramose in males of *Schizaspidia*, *Rhipipallus* and *Chalcura*. [Bouček 1988]

**41. Eupelmidae** (Fig. 42.27c). Body 1–10 mm; rarely strongly sclerotised or coarsely sculptured; usually dark coloured, often metallic; gena not posteriorly carinate; mesoscutum often impressed, at least posteriorly; mesopleuron inflated in females (except in some extralimital

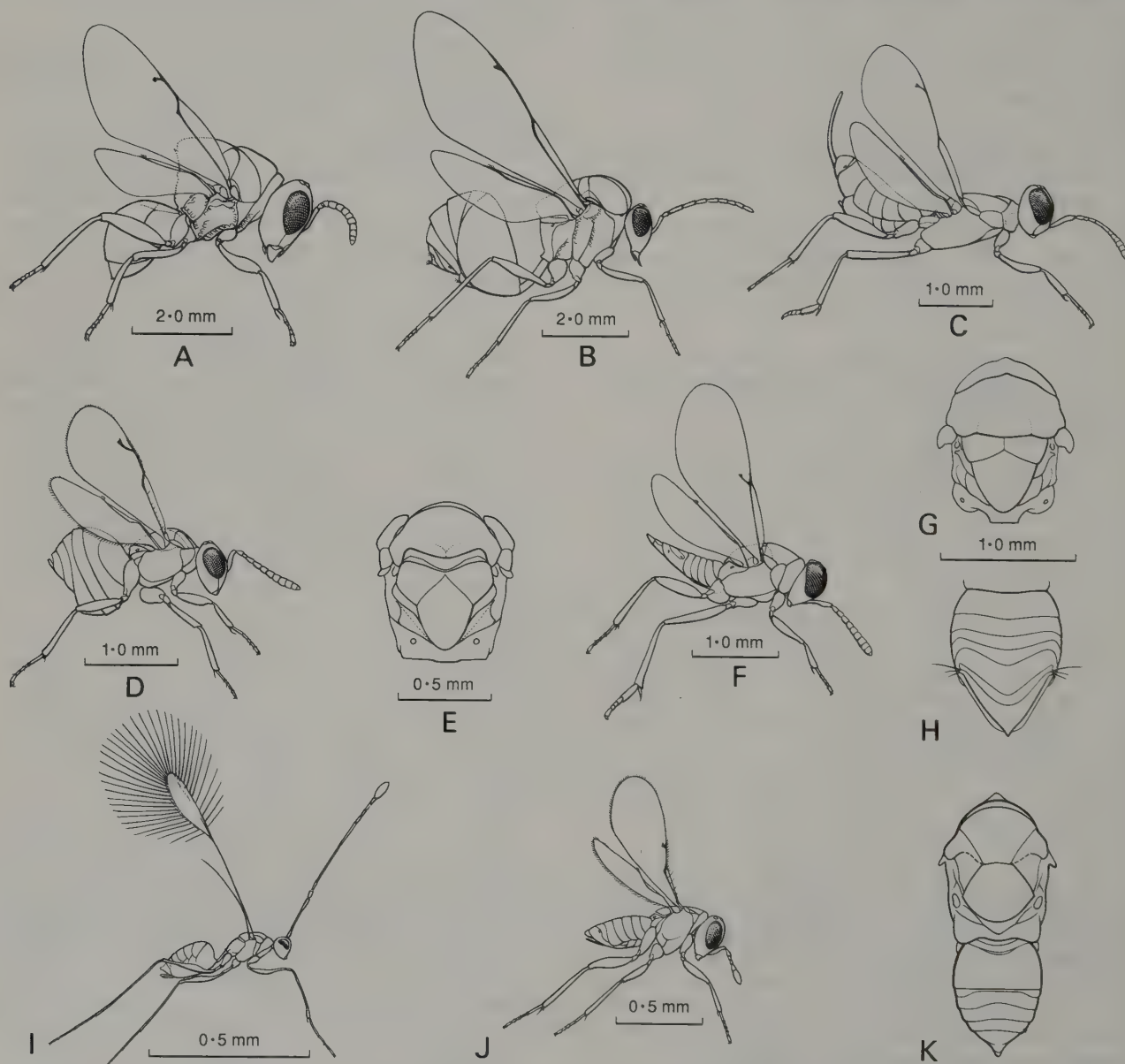


Fig. 42.27 Chalcidoidea: A, *Perilampus* sp., Perilampidae-Perilampinae; B, *Austeucharis* sp., Eucharitidae-Eucharitinae; C, *Eupelmus* sp., Eupelmidae-Eupelminae; D, *Tanaostigmodes* sp., Tanaostigmatidae; E, *Tanaostigmodes*, mesosoma, dorsal; F, *Psyllaephagus* sp., Encyrtidae-Encyrtinae; G, *Neocladia* sp., Encyrtidae-Encyrtinae, mesosoma, dorsal; H, *Neocladia* sp., metasoma, dorsal; I, *Mymar* sp., Mymaridae-Mymarinae; J, *Centrodora* sp., Aphelinidae; K, *Coccophagus* sp., Aphelinidae.

[A–D, F, I, J by S. Monteith; E, G, H by T. Nolan; K after Bouček 1988]



taxa), without sutures or coarse grooves; fore wings not longitudinally folded; sometimes brachypterous or micropterous; stigmal and postmarginal veins short relative to marginal vein; mid coxae close to hind coxae near posterior end of mesopleuron; usually with membranous area anterior to each mid coxa; legs usually slender, not dentate; mid leg with large tibial spur; mid basitarsus often stout, with 1 or 2 ventral rows of thickened setae; tarsi 5-segmented; cerci not advanced; ovipositor sometimes exerted.

In females there is often considerable mobility between mesosomatic sclerites and in some the mesosoma can be deformed considerably during jumping. In the latter the mesoscutum and mesoscutellum flex upwards so that the suture between them forms a transverse crest, the head and pronotum are pulled backwards against the mesoscutum, the mid legs are rotated forwards, and the metasoma is pulled forwards against the mesoscutellum. The enlarged mesopleuron and mid legs are also associated with jumping (Gibson 1986b). Eupelmids are most common in warmer regions.

#### Key to the Subfamilies of Eupelmidae Known in Australia

1. Mesopleuron enlarged and convex ..... 2  
    Mesopleuron not enlarged and convex .....  
        ..... EUPELMINAE (some ♂♂)
- 2(1). Mesoscutum in dorsal view quadrangular with conspicuous, rounded, anterolateral shoulders .....  
        ..... CALOSOTINAE  
    Mesoscutum in dorsal view not quadrangular, without conspicuous shoulders ..... 3
- 3(2). Mesosoma, in ventral view, with membranous region anterior to each mid coxa; mid tarsus without pegs or with rows of pegs along anteroventral and posteroventral edges ..... EUPELMINAE  
    Mesosoma, in ventral view, without membranous region anterior to each mid coxa; mid tarsus with row of pegs along anteroventral edge only .....  
        ..... METAPELMATINAE

CALOSOTINAE (25 spp.) parasitise larvae of Coleoptera in wood or (less commonly) grass stems. *Eusandalum* (11 spp.; usually with rasp-like protuberances on the head) and *Calosota* (10 spp.) are cosmopolitan.

METAPELMATINAE (22 spp.) lack the membranous area anterior to the mid coxae and are unable to rotate the mid legs forwards. *Metapelma* (2 spp.; hind tibiae and basitarsi flattened) parasitises wood-boring larvae of Cerambycidae and Buprestidae (COLE). Most *Neanastatus* (20 spp.; mesoscutellum with median sulcus) parasitise Cecidomyiidae (DIPT) in grasses and herbaceous plants; an Australian species has been reared from galls on *Eremocitrus*.

Males of EUPELMINAE (14 genera; 130 spp.) resemble those of some Torymidae or Pteromalidae. Females of many species are wing reduced. In *Anastatus* (40 spp.) the posterior margin of the apical gastral tergum is often pale and slightly upturned; Australian species have been

reared from mantid and cockroach oothecae, from eggs of Heteroptera and Lepidoptera, and from puparia of parasitic pipunculid flies (some extralimital species are hyperparasitic via Braconidae). *Eupelmus* (50 spp.; Fig. 42.27C) parasitises small Noctuidae (LEPI) and Curculionidae (COLE), mantid oothecae and the immature stages of Cecidomyiidae (DIPT) in grasses. [Bouček 1988]

**42. Tanaostigmatidae** (Figs 42.27D, E). Body 0.7–3.8 mm; not strongly sclerotised, not coarsely punctate; dark or pale coloured, sometimes partially or wholly metallic; gena not posteriorly carinate; prepectus greatly enlarged, projecting forward to partially cover lateral panel of pronotum; mesopleuron large, convex, without sutures; notauli usually complete, well defined, meeting posteriorly to form a V or Y; fore wings not longitudinally folded; marginal vein usually longer than stigmal vein; legs slender; mid coxae almost mid-way between fore and hind coxae; mid tibia with stout spur; mid basitarsus with 2 ventral rows of thickened setae; tarsi 5-segmented; cerci not advanced; ovipositor not exerted.

As in many Eupelmidae the mesosoma can be contracted by flexion at the mesoscutal-mesoscutellar suture and the mid legs can rotate forward. *Tanaostigmatodes* (10 spp.) is cosmopolitan and phytophagous, either as a gall former or as a gall inquiline. Australian tanaostigmatids have been reared from pods of various Fabaceae and from galls on *Leptospermum*. [LaSalle 1987]

**43. Encyrtidae** (Figs 42.27F–H). Body 0.5–5 mm; not strongly sclerotised, usually not coarsely sculptured; dark or pale, often metallic; gena rarely posteriorly carinate; antennae 5–11-segmented; prepectus not greatly enlarged; notauli rarely present; axillae large, usually contiguous medially; mesopleuron large, convex, without sutures or coarse grooves; fore wings not longitudinally folded; marginal and postmarginal veins often shorter than stigmal vein; legs usually slender; mid coxa close to fore coxa, attached at about middle of mesopleuron; mid tibia with long spur; cerci usually advanced; ovipositor rarely exerted. A few species are micropterous or apterous.

Encyrtidae are mostly endoparasitic in Hemiptera or insect larvae and are particularly diverse in warm, drier regions.

Paratergites (lateral subdivisions of the metasomal terga) are present in TETRACNEMINAE. *Tetracnemus* (2 spp.), *Leptomastix* (3 spp.), *Callipteroma* (3 spp.), *Charitopus* (3 spp.) and *Anagyrus* (12 spp.) all parasitise Pseudococcidae (HEMI). *Anagyrus* also attacks Coccinellidae (COLE). *Ananusia* (2 spp.) occurs in ant nests where they probably parasitise ant-associated Pseudococcidae. Possibly *Charitopus* and related genera are the most primitive Encyrtidae. *Charitopus*, in particular, resembles Tanaostigmatidae or Eupelmidae in having a relatively long marginal vein, well-developed notauli, cerci near the apex of the gaster and a membranous area around the mid coxae so that the mid legs can be rotated forwards.

ENCYRTINAE lack paratergites and are morphologically and biologically more diverse than Tetracneminae. *Encyrtus* (2 spp.), *Metaphycus* (20 spp.) and *Microterys* (10 spp.) are common parasites of Coccidae (HEMI).



*Cheiloneurus* (25 spp.) parasitises aphelinid and encyrtid parasites of various coccoids and dryinid parasites of leafhoppers (HEMI). *Saprencyrus* (1 sp.), associated with *Cylindrococcus* (HEMI: Eriococcidae) galls on *Casuarina* and *Aenasiella* (7 spp.), reared from *Apiomorpha* (Eriococcidae) galls on *Eucalyptus*, are both endemic. *Neocladia* (4 spp.), in which the hind tibiae are leaf-like, and *Eugahania* (1 sp.), with a notched costal margin, parasitise nymphs of Cicadellidae (HEMI). Adult *Neocladia* are sometimes attracted to sunlit tree trunks. All *Psyllaephagus* (106 spp.) are parasitic or hyperparasitic on Psyllidae (HEMI).

*Tachinaephagus* (2 spp.) parasitises larvae and puparia of synanthropic Diptera. *Syrphophagus* (15 spp.) attacks either aphids or the larvae of aphidophagous Syrphidae (DIPT).

*Ooencyrtus* (15 spp.) develops in eggs of Lepidoptera, Heteroptera and spiders. *Fulgoridicida* (5 spp.) and *Xenoencyrtus* (4 spp.) are endemic with species in eggs of Eurybrachyidae and Pentatomidae (HEMI) respectively. Species of several genera parasitise egg masses of paropsine Chrysomelidae (COLE). *Amira* (1 sp.) attacks spider egg masses, and *Comperia* (1 sp.) cockroach oothecae.

*Copidosoma* (17 spp.) and *Paralitomastix* (3 spp.) are polyembryonic parasites of lepidopterous larvae. *Coelophencyrtus* (1 sp.) parasitises larvae of *Exoneura* (Anthophoridae) in their nests and *Ixodiphagus* (1 sp.) nymphal ticks (Acarina: Ixodidae). [Noyes and Hayat 1984; Noyes 1988]

**44. Aphelinidae** (Figs 42.27J, K). Body 0.3–2.5 mm; weakly sclerotised and without coarse microsculpture; usually non-metallic; dark or pale coloured; gena not posteriorly carinate; antennae 3–9-segmented; mesopleuron sometimes inflated and without sutures; notauli distinct; axillae widely separated, anterior margin usually advanced; fore wings not longitudinally folded, occasionally absent; fore wing marginal vein usually very long relative to stigmal and postmarginal veins; legs usually slender; mid coxae nearer to hind coxae than to fore coxae; tarsi 4- or 5-segmented; metasoma broadly sessile; cerci not advanced; ovipositor usually not strongly exerted.

Aphelinids are mostly parasitic on sternorrhynchous Hemiptera and many are important agents for the biological control of pests.

All *Aphytis* develop ectoparasitically and all *Aphelinus* and *Centrodora* as endoparasites. In some species of other genera females develop as endoparasites and males as ectoparasites, or the two sexes of the one species develop similarly but in different hosts. Occasionally females are parasites and males are hyperparasites, even via larvae and pupae of their own species.

Genera (and their known hosts) represented in Australia include *Aphytis* and *Pteroptrix* (Diaspididae), *Aphelinus* (aphids), *Coccophagus* (Coccidae, Pseudococcidae, Eriococcidae), *Eretmocerus* and *Cales* (Aleyrodidae), *Encarsia* (Aleyrodidae, Diaspididae), *Marietta* (Encyrtidae, Aphelinidae parasitic on scale insects), *Centrodora* (eggs of Orthoptera, Hemiptera and Lepidoptera) and *Eutrichosomella* (Encyrtidae parasitic in cockroach oothecae).

*Euryischia*, *Myiocnema* and related genera superficially resemble Elasmidae and differ from other aphelinid genera in having very large hind coxae, often spinose hind tibiae and relatively long stigmal and postmarginal veins. *Euryischia* and *Myiocnema* are hyperparasites via various Diptera or Braconidae on aphids, psyllids or scale insects. [Hayat 1983; Viggiani 1984]

**45. Signiphoridae** (Fig. 42.28D). Body 0.5–2 mm; black or yellow, usually non-metallic; not strongly sclerotised, smooth; dorsoventrally flattened; gena not posteriorly carinate; antennae 4–7-segmented; funicle segments very short, ring-like; club long, unsegmented; prepectus large, flat; notauli absent; mesoscutellum band-like, axillae indistinct; mesopleuron enlarged, convex; propodeum with large, triangular, median area; fore wings not folded, often with long marginal setae but without setae on wing membrane; marginal vein long relative to very short stigmal vein; postmarginal vein absent; legs slender; tarsi 5-segmented; mid femur and tibia with long spines; mid tibia with long, toothed spur; metasoma broadly sessile; cerci not advanced; ovipositor not strongly exerted.

One Australian signiphorid is hyperparasitic via *Psyllaephagus* in psyllids (HEMI). Extralimital species include hyperparasites of coccoids and aphids and some primary parasites of Pseudococcidae (HEMI) and Diptera. [Woolley 1988]

**46. Tetracampidae**. Body 1–2 mm; not strongly sclerotised, mostly smooth; metallic; genae not posteriorly carinate; occipital carina usually present; antennae 11–12-segmented; pronotum usually large and bell-shaped or conical with its hind margin closely applied to mesoscutum; notauli present; mesoscutellum with pair of long setae; axillae not advanced; mesopleuron not enlarged; marginal vein long relative to stigmal vein; postmarginal vein long; submarginal vein distally weakened; legs slender; fore tibial spur weak, bifid; tarsi 5-segmented in females; 4- or 5-segmented in males; cerci not advanced; ovipositor not exerted.

Tetracampids parasitise leaf-mining dipterous larvae or the eggs of leaf-feeding Chrysomelidae (COLE) or Symphyta. Only TETRACAMPINAE are represented in Australia and these are rare. [Bouček 1988]

**47. Eulophidae** (Figs 42.25H, I). Body 0.5–6 mm; often weakly sclerotised, shrivelling after death; usually not coarsely sculptured; often metallic; colours variable; antennae with reduced number of segments (at most 12, usually fewer); funicle with 4 or fewer segments; male antennae sometimes with rami; head often with frontal grooves or desclerotised lines; gena not posteriorly carinate; occipital carina absent; notauli usually distinct; axillae advanced; mesopleuron not inflated; mesoscutellum often with paired, submedian grooves; fore wings not longitudinally folded; marginal vein long relative to stigmal and postmarginal veins; legs slender; fore tibial spur short, straight; tarsi 4-segmented in both sexes; cerci not advanced; ovipositor not exerted.

Eulophidae include ecto- and endoparasites and hyperparasites of a variety of hosts, especially larvae of Lepidoptera and Diptera in leaf mines. A few are phytophagous. The family is particularly diverse in Australia.



*Key to the Subfamilies of Eulophidae Known in Australia*

1. Notauli incomplete, their posterior halves absent or represented by broad depressions ..... 2
- Notauli distinct, reaching or almost reaching mesoscutellum ..... 3
- 2(1). Mesoscutellum with 2 or more pairs of long setae, sometimes with additional smaller setae; submarginal vein of fore wing dorsally with 4 or more long setae ..... EULOPHINAE (pt)
- Mesoscutellum with 1 pair of setae; submarginal vein of fore wing dorsally with 2 long setae ..... ENTEDONINAE (pt)
- 3(1). *Either* axillae strongly, acutely advanced; *or* axillae moderately advanced and anterior pair of mesoscutellar setae near to or behind middle of mesoscutellum ..... TETRASTICHINAE (pt)
- Axillae not strongly, acutely advanced; or if approaching this condition then anterior setae of mesoscutellum in anterior third of mesoscutellum ..... 4
- 4(3). Submarginal vein of fore wing usually with 2 long setae dorsally (rarely 1), mesoscutellum with 1 pair of setae ..... ENTEDONINAE (pt)
- Submarginal vein of fore wing usually with more than 2 long setae dorsally, if with only 1 or 2 then mesoscutellum with 2 pairs of setae ..... 5
- 5(4). Submarginal vein distally smoothly curving into marginal vein ..... EULOPHINAE (pt)
- Submarginal vein distally interrupted, not smoothly curving into marginal vein ..... 6
- 6(5). Mesoscutellum with 2 or 4 longitudinal grooves ..... TETRASTICHINAE (pt)
- Mesoscutellum without longitudinal grooves ..... EUDERINAE

EULOPHINAE include the most primitive genera. The submarginal vein continues unbroken to the marginal vein and the apical and preapical metasomal terga are fused. *Anselmella*, with unusual, multisegmented antennae, develops in seeds of *Eugenia*. Most (e.g. *Sympiesis*, *Cirrospilus*, *Hemiptarsenus*) are ectoparasites of leaf-mining or stem-tunnelling insects. *Ophelimus* (50 spp.) is commonly reared from galls on *Eucalyptus*. *Euplectrus* (12 spp.; Fig. 42.25H), with large hind tibial spurs, is a gregarious ectoparasite of exposed-feeding lepidopterous larvae and exceptional among the Chalcidoidea in forming a cocoon. *Elachertus* also parasitises lepidopterous larvae.

In EUDERINAE the submarginal vein is interrupted distally, there are often 3 distinct hair lines radiating from the stigmal knob, and the notauli are deep and narrow. Extralimital *Euderus* spp. parasitise leaf-mining or stem-boring Lepidoptera and Coleoptera or are hyperparasitic via Braconidae. Some *Astichus*, with patterned wings, have been reared from fungi where they parasitise Ciidae.

TETRASTICHINAE, in which the submarginal vein is interrupted, the notauli are deep and straight, and the mesoscutellum usually has a pair of submedian grooves, are abundant and ubiquitous. Australian species most commonly parasitise galls, or the eggs, larvae or pupae of Lepidoptera and Diptera. *Aprostocetus* and *Tetrastichus*, both with diverse hosts, are the largest Australian genera.

*Quadrastichodella* is phytophagous in eucalypt seed capsules. *Melittobia* is a polyphagous parasite in nests of aculeate Hymenoptera.

ENTEDONINAE, with modified notauli and the submarginal vein interrupted, are the most derived eulophids. Some (e.g. *Pediobius*, *Entedon*, *Apleurotropis*) are relatively well sclerotised, others (e.g. *Omphale*) less so. Most are endoparasitic in eggs and young larvae of Lepidoptera, Coleoptera and Diptera in plant tissue. *Pediobius* has also been reared from pupae of parasitic Hymenoptera and Diptera, spider egg sacs and mantid oothecae. *Ceranisis* parasitises Thysanoptera. [Boucek 1988]

**48. Elasmidae** (Fig. 42.25I). Body 1–3 mm; not strongly sclerotised, not coarsely sculptured; dark coloured or patterned with yellow or orange, sometimes metallic; antennae 8-segmented; male antennae ramose; genae not posteriorly carinate; axillae advanced; fore wing wedge-shaped, not longitudinally folded; marginal vein long relative to submarginal, postmarginal and stigmal veins; hind coxa greatly enlarged, flattened; legs otherwise slender; tarsi 4-segmented; metasoma sessile, tapering, triangular in cross-section; cerci not advanced; ovipositor not exerted.

Elasmids are mostly ectoparasites of larvae of Lepidoptera or hyperparasites of these via Braconidae or Ichneumonidae. A Nearctic species parasitises *Polistes* (Vespidae). Dark setae on the otherwise pale hind tibia are arranged in diamond-shaped patterns in *Elasmus* (50 spp.) and in wavy lines in *Austelasmus* (10 spp.). [Riek 1967]

**49. Trichogrammatidae** (Figs 42.28A–C). Among the smallest insects known, 0.15–1 mm; not strongly sclerotised, mostly smooth; non-metallic, often pale coloured; genae not posteriorly carinate; antennae shorter than head and thorax, 4–9-segmented, often with a very short funicle and large club; pronotum not conspicuous in dorsal view; mesosoma dorsally sparsely setose; notauli distinct; axillae advanced; mesopleuron not enlarged; fore wing often with long marginal cilia and often with setae of disc arranged in radiating lines; postmarginal vein absent; stigmal vein often short or absent; legs slender; tarsi 3-segmented; fore tibial spur short and straight; fore basitarsus without a strigil comb; cerci not advanced; ovipositor rarely exerted.

Trichogrammatids are primary endoparasites in the eggs of Lepidoptera, Hemiptera, Thysanoptera and (less commonly) Coleoptera, Neuroptera, Diptera and Odonata. Few Australian species have been reared. Because of their small size trichogrammatids are distributed readily by wind.

In TRICHOGRAMMATINAE the aedeagus has accessory structures such as a phallobase, parameres and volsellar digiti. *Trichogramma* (7 spp.) and *Trichogrammatoidea* (3 spp.) are cosmopolitan genera which include parasites of economically important Noctuidae (e.g. *Helicoverpa*), Tortricidae and Pyralidae (LEPI) (Nagarkatti and Nagaraja 1977).

The aedeagus is simple and tubular in OLIGOSITINAE. *Oligosita* (33 spp.) has few discal setae (Viggiani 1976). Adults of *Prestwichia* (1 sp.) can swim under water and

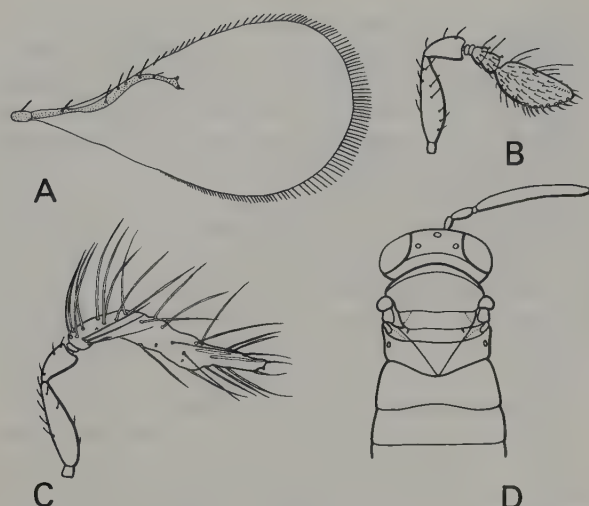


Fig. 42.28 Chalcidoidea: A, *Trichogramma* sp., Trichogrammatidae, fore wing; B, C, *Trichogramma* sp., ♀, ♂ antenna; D, *Signiphora* sp., Signiphoridae. [A–C after Doutt and Viggiani 1968; D after Bouček 1988]

females oviposit in the eggs of Zygoptera (ODON). [Doutt and Viggiani 1968]

**50. Mymaridae** (Fig. 42.27t). Usually minute, 0.2–1 mm, occasionally reaching 4 mm; not strongly sclerotised; finely sculptured or apparently smooth; generally non-metallic; gena not posteriorly carinate; antennal sockets usually wide apart and close to compound eyes; head with transverse sulcus above the antennal sockets, and longitudinal sulci above and anterior to compound eye; mandibles endodont, sometimes elongate; antennae longer than head and thorax (except in *Stethynium*), slender, 8–13-segmented, filiform in males, females with conspicuous club; pronotum generally not conspicuous in dorsal view, rarely reaching to tegula; prepectus usually present, sometimes very small or fused to pronotum; notauli present or absent; axillae usually not advanced; mesopleuron not inflated; fore wing often slender, occasionally stalked and with long, marginal cilia, always with a *hypochaeta* (a specialised, distally hooked, posteriorly directed, ventral seta inserted near the costal margin); usually marginal and stigmal veins short and postmarginal vein absent; hind wing very slender, usually stalked (membrane absent from base); legs slender; tarsi 4- or 5-segmented; fore leg with well-developed strigil; cerci not advanced; ovipositor rarely exerted.

Mymarids parasitise insect eggs, especially those more or less concealed (e.g. in plant tissue, under scales, in soil). Eggs of auchenorrhynous Hemiptera, Psocoptera, Curculionidae and Tettigoniidae are the most common hosts. Several species are important biocontrol agents, e.g. *Anagrus frequens* introduced from Australia to Hawaii to control sugar cane planthopper *Perkinsiella saccharicida* (HEMI: Delphacidae), *Anaphes diana* introduced from Europe to Australia to control *Sitona*

*discoideus* (COLE: Curculionidae) on lucerne. Because of their small size mymarids are often dispersed by wind. The tarsi are 5-segmented in GONATOCERINAE and 4-segmented in MYMARINAE. The metasoma is either petiolate or broadly attached. Most described Australian species belong to the cosmopolitan genera *Gonatocerus*, *Alaptus*, *Anagrus* and *Polynema*. *Stethynium* is primarily Australian. [Huber 1986]

### Superfamily CHRYSIDOIDEA

Almost exclusively parasitic and generally of small size. Antennae primitively 13-segmented in both sexes; secondarily multisegmented in Sclerogibbidae and reduced in Embolemidae, Dryinidae and some Bethylidae. Palpal formula 6-4 retained only in the Scolebythidae. In Scolebythidae and some wing-reduced forms in other families the propleura are prolonged anteriorly to form a long neck projecting in front of the pronotum; dorsally the propleura are either separated by membrane or fused. This adaptation allows a more mobile head. The pronotum is mobile on the mesothorax and an independent prepectus is present. The femora are often enlarged in female Bethylidae, Embolemidae and Dryinidae, and the fore femora massively so in female Sclerogibbidae. Males of the extralimital Plumariidae have the most complete venation, with 8 closed cells in the fore wing and 3 closed cells in the hind wing. The venation is variously reduced in other families, reaching extremes in Aphelopinae (Dryinidae), Lobo-scelidiinae (Chrysidae) and some Bethylidae in which there is only one closed cell in the fore wing. M+Cu and all cross-veins are lost from the hind wing in all except male Plumariidae. In most families there are 7 visible metasomal terga. This is reduced to 4 (females) or 5 (males) or fewer in Chrysidae in which the more posterior segments are telescoped within preceding ones. In the ovipositor, an articulation within the 2nd valvifer is an autapomorphy for the superfamily. Other autapomorphies are the loss of veins 2A and 3A and the jugal lobe from the hind wing and the loss of *1m-cu* and *3r-m* from the fore wing. All of the non-plumariid families are united by reduced venation and (apart from Scolebythidae) reduced palpal formula. The loss of the furcula from the ovipositor is a synapomorphy of the Sclerogibbidae, Embolemidae and Dryinidae. Possibly Embolemidae and Dryinidae are sister groups; both have 10-segmented antennae, and in both larvae are initially endoparasitic and later ectoparasitic on nymphs of auchenorrhynous Hemiptera. Bethylidae and Chrysidae are sister groups with a similar tube-like ovipositor in which the articulation between the 2nd valvifer and the 2nd valvulae has been lost. Bethylidae, Chrysidae and Dryinidae are the most commonly collected families. Most chrysoid families include some wingless females, these often being very ant-like. Plumariidae, in which females are apterous and males fully winged, occur only in arid regions of South America and south-west Africa. [J. M. Carpenter 1986]

### Key to the Families of Chrysidoidea Known in Australia

1. 'Neck' elongate (Fig. 42.29A), propleura visible from above; prosternum both larger than fore coxa and diamond-shaped ..... **Scolebythidae** (p. 971)



- 'Neck' short (Figs 42.29B–K), propleura covered dorsally by pronotum; prosternum not as above ..... 2
- 2(1). Antennae 15–39-segmented, inserted beneath frontal shelf (Fig. 42.29B) ..... **Sclerogibbidae** (p. 971)
- Antennae 10–13-segmented, not inserted beneath frontal shelf ..... 3
- 3(2). Antennae 10-segmented ..... 4
- Antennae 12- or 13-segmented ..... 5
- 4(3). Antennae inserted remote from mouth on frontal prominence (Fig. 42.29E); fore tarsus normal ... **Embolemidae** (p. 971)
- Antennae inserted near mouth, not on frontal prominence; fore tarsus of female often chelate (Figs 42.29C, D) ..... **Dryinidae** (p. 971)
- 5(3). Vertex posteriorly prolonged; scape, femora, tibiae with translucent flanges (Fig. 42.29I) ..... **Chrysididae** (pt, p. 973)
- Vertex not posteriorly prolonged; flanges absent ..... 6
- 6(5). Pronotum extending posteriorly to tegula (Fig. 42.29F) or tegula absent (Fig. 42.29G); metasoma with 7 or 8 visible terga ..... **Bethylidae** (p. 973)
- Pronotum not extending posteriorly to tegula (Figs 42.29H, J, K); tegula always present; metasoma with 3–6 visible terga ..... **Chrysididae** (pt, p. 973)

**51. Scolebythidae** (Fig. 42.29A). Body slender, 4.5–8 mm, dorsoventrally flattened; head on distinct 'neck'; prosternum large; fore coxae posteriorly produced; pterostigma swollen. *Ycaploca evansi* from Australia and South Africa is probably parasitic on larvae of Cerambycidae (COLE) and can be collected from tunnels in wood. *Clystopsenella* occurs in Australia and South America. [Brothers 1981]

**52. Sclerogibbidae** (Fig. 42.29B). Small (2.3–6 mm). Females apterous with enlarged fore femora; head subtriangular with antennae inserted close to clypeus beneath frontal shelf. Male fully winged with 5 or 6 closed cells in fore wing. Antennae 15–39-segmented; scape short. Ectoparasitic on immature Embioptera. The sclerogibbid larva, attached dorsally at intersegmental membranes, eventually kills the host and pupates in a cocoon within the silken, embiid tunnels. [Yasumatsu 1958]

**53. Embolemidae** (Fig. 42.29E). Small (1.6–5 mm). In Australian species females brachypterous with particularly enlarged fore femora and very long scapes; males fully winged. Antennae 10-segmented. Tibial spur formula 1-2-2. T3 with pair of oval-shaped areas differentiated by colour and microsculpture. Collected in damp habitats, including litter. A Nearctic species has been reared from nymphs of Achilidae (HEMI) in rotting wood. [O. W. Richards 1939; Valentine and Walker 1983; Bürgis 1987]

**54. Dryinidae** (Figs 42.29C, D). Small (1.5–10 mm); antennae 10-segmented; fore leg of female (except in Aphelopinae and extralimital Biaphelopinae) with chela formed by elongate lobe of 5th tarsal segment and one enlarged tarsal claw (Fig. 42.70), the 2nd tarsal claw is rudimentary or absent; sexual dimorphism sometimes marked (especially in Dryininae and Gonatopodinae). Parasites of adults and nymphs of leafhoppers (HEMI: Auchenorrhyncha), species sometimes attacking several related genera or families of hosts. Female dryinids use their chelae to catch and hold hosts which they sting into temporary paralysis. One or more eggs are laid between sclerites of the host thorax or abdomen. The dryinid larva is U-shaped and feeds externally within a sac (*thylacium*) of its own shed larval skins (Fig. 3.28). Parasitised hosts undergo no further moults. Pupation takes place either on the host plant or in the soil or litter beneath the host plant. Female Aphelopinae lack chelae and use their fore and mid legs to hold hosts during oviposition. The early instar

aphelopine larva feeds through a trophamnion and at least the 1st instar is endoparasitic. An extralimital aphelopine is polyembryonic. Female dryinids sometimes kill and feed on leafhoppers. Many are ant mimics and are found with ants as the latter attend leafhoppers for honeydew. One *Anteon* appears to be myrmecophilic and may be fed trophallactically by ants.

#### Key to the Subfamilies of Dryinidae Known in Australia

1. Fore tarsus not chelate (♂♂ or ♀♀) ..... 2
- Fore tarsus chelate (♀♀ only) ..... 3
- 2(1). Fore wing with only costal cell completely enclosed by pigmented veins; occipital carina complete ..... 4
- ..... APHELOPINAE (♀♀, ♂♂)
- Fore wing with costal and 1 or 2 basal cells enclosed by pigmented veins; if only with costal cell enclosed, occipital carina absent ..... 5
- ..... ♂♂ of remaining subfamilies
- 3(1). Wings absent ..... GONATOPODINAE (pt)
- Wings present, sometimes small ..... 4
- 4(3). Mid tibia without apical spur ..... 5
- Mid tibia with 1 apical spur ..... 6
- 5(4). Each mandible with 4 teeth; pronotum without posterior lobe directed towards tegula ..... 6
- ..... GONATOPODINAE (pt)
- Each mandible with 1 tooth; pronotum with posterior lobe directed towards tegula ..... TRANSDRYININAE
- 6(4). Flagellar segments 3–8 each with tufts of hairs ..... 7
- ..... THAUMATODRYININAE
- Flagellar segments without tufts of hairs ..... 7
- 7(6). Metasoma with distinct, tubular petiole .... BOCCHINAE
- Metasoma without distinct, tubular petiole ..... 8
- 8(7). Fore trochanter at most 2 times longer than wide ..... 8
- ..... ANTEONINAE
- Fore trochanter elongate, more than 2 times longer than wide ..... DRYININAE

APHELOPINAE (*Aphelopus*, 2 spp.) are small (2 mm or less), mostly dull coloured; females and males are very similar in appearance. ANTEONINAE (*Anteon*, 24 spp.; Fig. 42.29D) parasitise Cicadellidae and can be common on tree trunks. All Australian BOCCHINAE (*Bocchus*, 5 spp.) have a long, tubular petiole and parasitise Fulgoridae. THAUMATODRYININAE (*Thaumatomyia*, 2 spp.) are 6–7 mm long, pale coloured and attracted to light in northern regions; they parasitise Flatidae. DRYININAE (*Dryinus*,

24 spp.; *Mesodryinus*, 1 sp.) include attractive species, often up to 10 mm long and with patterned fore wings; Flatidae, Ricianiidae and Dictyopharidae are hosts. The TRANSDRYININAE is a monotypic, endemic subfamily. The GONATOPODINAE include *Neodryinus* (3 spp.; parasitic on

Flatidae, Ricianiidae and Nogodinidae) and *Echthrodelphax* (4 spp.; parasitic on Delphacidae), both with well-developed wings, and several genera in which the females are apterous and very ant-like with a pronounced constriction in the middle of the mesosoma. The latter,



Fig. 42.29 Chrysidoidea: A, *Ycaploca evansi*, Sclerbythidae; B, *Sclerogibba* sp., Sclerogibbidae; C, *Gonatopus* sp., Dryinidae, ♀; D, *Anteon* sp., Dryinidae, ♀; E, *Embolemus* sp., Embolemidae; F, *Eupsenella* sp., Bethyidae; G, *Apenesia* sp., Bethyidae; H, *Primeuchroeus* sp., Chrysididae-Chrysidinae; I, *Loboscelidia* sp., Chrysididae-Loboscelidiinae; J, *Myrmecomimesis* sp., Chrysididae-Amiseginae, ♀; K, *Myrmecomimesis* sp., ♂.

[A by T. Nolan; B–F, H, J, K by T. Binder; G by A. Hastings; I by S. P. Kim]



which are often found in litter, parasitise Delphacidae, except for *Gonatopus* (9 spp.; Fig. 42.29C) which attacks Cicadellidae. Biaphelopinae, Conganteoninae and Apodryininae are not recorded from Australia. [Olmi 1984]

**55. Bethylidae** (Fig. 42.29F, G). Small (1–10 mm) parasites of larvae and occasionally pupae of Coleoptera and Lepidoptera in concealed situations. Adults more or less flattened with stout legs. Head distinctive, combining broad genal and postgenal bridges with usually relatively small eyes and prognathy. Wings often reduced or absent, especially in females; some species polymorphic (H. E. Evans 1963). Host paralysis, either temporary or permanent. Some extralimital species drag the host to sheltered positions before oviposition; one Nearctic *Epyris* constructs a nest (Rubink and Evans 1980). One or more eggs per host; larvae feed externally, eventually forming a cocoon. Females of several non-Australian species remain with the host and defend their progeny.

*Key to the Subfamilies of Bethylidae Known in Australia  
(forms with well-developed wings only)*

1. Basal vein (transverse vein defining distal ends of cells R and M+CuA, cf. Fig. 42.8D) of fore wing giving rise to vein or subtending small cell (Fig. 42.29F) ..... BETHYLINAE
- Basal vein without vein or cell ..... 2
- 2(1). Metanotum well developed, anteriorly with transverse groove or fovea; mesoscutellum and propodeum not in contact ..... PRISTOCERINAE
- Metanotum not well developed, without groove or fovea; mesoscutellum and propodeum medially in contact ..... EPYRINAE

Wing-reduced forms are often difficult to place to subfamily. Some apterous females are similar to female Thynninae but usually lack spiniform setae on the hind tibiae. Many genera are cosmopolitan. Mesitiinae (pronotum usually with median groove, propodeum posterolaterally spinose) are absent from Australia.

Australian PRISTOCERINAE occur in soil, litter, wood and under bark and probably parasitise coleopterous larvae. Females apterous, without tegulae, often with very small eyes, ant-like in appearance and sometimes collected in association with ants. Males macropterous. Propodeum anteriorly strongly constricted in *Pseudisobrachium* (1 sp.). Metasoma distinctly petiolate in *Dissomphalus* (2 spp.). Mid tibiae with spiniform setae in *Apenesia* (15 spp.; Fig. 42.29G).

EPYRINAE parasitise coleopterous larvae. Cephalonomiini have 12-segmented antennae. *Cephalonomia* (3 spp.) has been reared from Ciidae in fungi and from grain beetles; both sexes sometimes wing reduced but if fore wing present, radial vein absent. Radial vein present in *Plastanoxus* (1 sp.). Females micropterous in Sclerodermini. *Sclerodermus* (2 spp.) parasitises larvae in wood. *Lepidosternopsis* (2 spp.) is known also from islands near South America. Epyrini generally have fully developed wings. *Rhabdepyris* (25 spp.), with a transverse, mesoscutellar groove and well-developed notauli, includes the largest Australian bethylids; one species is associated with ants. *Holepyris* (2 spp.) has a mesoscutellar groove

and weak notauli and *Epyris* (6 spp.) a pair of mesoscutellar pits. *Cephalonomia*, *Plastanoxus* and *Holepyris* each include cosmopolitan parasites of stored grain beetles.

BETHYLINAE parasitise lepidopterous larvae, especially those in leaf rolls and within stems. Marginal cell closed in *Sierola* (12 spp., submarginal vein thickened near pterostigma) and *Eupsenella* (4 spp., submarginal vein not thickened; Fig. 42.29F) and open in *Goniozus* (12 spp.). [H. E. Evans 1978; Hawkins and Gordh 1986]

**56. Chrysididae** (Plate 5, V; Figs 42.29H–K). Small to large (2.5–22 mm). Terminal metasomal segments forming a telescopic tube which is usually concealed by the preceding 6 or fewer terga. Biologically diverse. Chrysidinae parasitise almost exclusively nests of Sphecidae and Eumeninae (Vespidae); Amiseginae and Loboscelidiinae eggs of Phasmatodea; and the extralimital Cleptinae larvae of Tenthredinidae. Females of Chrysidinae have 3 exposed, usually heavily sclerotised, metasomal terga and flat or concave sterna; they can roll into a defensive ball if attacked by nest-building wasps or bees. The other subfamilies, which attack less aggressive hosts, lack this protective adaptation. Larvae have 2–4 mandibular teeth and at least some spin cocoons.

*Key to the Subfamilies of Chrysididae Known in Australia*

1. Metasoma with 4–6 exposed terga (Figs 42.29I–K), ventrally convex ..... 2
- Metasoma with 3 exposed terga (Fig. 42.29H), ventrally flat or concave ..... CHRYSIDINAE
- 2(1). Vertex posteriorly prolonged (Fig. 42.29I); scapes, femora and tibiae with translucent flanges; fully winged in both sexes, venation of fore wing not reaching costal margin ..... LOBOSCELIDIINAE
- Vertex not posteriorly prolonged (Figs 42.29J, K); flanges absent; fore wing of female minute; ♂♂ fully winged, venation of fore wing reaching costal margin ..... AMISEGINAE

CHRYSIDINAE (58 spp.). Metallic green or blue; heavily sclerotised and coarsely sculptured. Usually female oviposits into host cell while it is still open and being provisioned. Either the chrysidine larva hatches almost immediately and feeds on cell contents or hatching is delayed until the host reaches the prepupal stage. Some *Chrysis* can chew into sealed mud cells. In Elampini (2 spp.) the radial vein is very short and sclerotised for less than half the length of the marginal cell. Most Australian species belong to the Chrysidini in which the radial cell is much longer. *Stilbum cyanurum* (Plate 5, V), the largest (up to 22 mm) and most frequently collected species, is widespread throughout the world (except North and South America) and may have been introduced accidentally by humans. It is a parasite of *Sceliphron* and *Abispa*. The apex of the metasoma is entire in *Primeuchroeus* (30 spp.; Fig. 42.29H) and dentate in *Chrysis* (27 spp.). *Praestochrysis* (2 spp.) is unusual in parasitising larvae of Limacodidae and Bombycidae (LEPI); *P. lusca* is a pest of *Bombyx mori* in China. [Bohart and Kimsey 1982]

LOBOSCELIDIINAE (2 spp.; Fig. 42.29I) from the Indo-Oriental region and northern Australia are smooth, pol-

ished and grotesque, with a prolonged vertex, flanges, large tegulae, wrinkled and yellowed fore wings and reduced venation. One species has been reared from eggs of *Ctenomorphodes tessulatus*. [Day 1979; Krombein 1983]

Females of Australian AMISEGINAE (15 spp.; Figs 42.29J, K) have fore wings smaller than the tegulae, a large pronotum and small mesoscutum. They search in leaf litter for phasmatid eggs, in which they chew a hole to enable oviposition. The subfamily occurs also in the Indo-Oriental region, southern Africa and the Americas (Riek 1955c; Krombein 1957, 1983).

### Superfamily VESPOIDEA

Mostly medium to large sized; and including parasitic, predatory and melliferous species. Formicidae and some Vespidae are eusocial. Morphologically diverse. There are tendencies towards reduction and invagination of the metapostnotum, posterior approximation of the propleura and shortening of the prepectus. Tiphidae, Scoliidae and Mutillidae are superficially similar, stoutly built, often

hairy, frequently fossorial parasites. The distal position of cross vein *cu-a* in the hind wing and some ovipositor and larval character states suggest a close relationship between the Tiphidae, Mutillidae and Sapygidae. Pompilidae and Rhopalosomatidae appear to be sister groups with a similar development of the hind tibial calcar. The pronotum is mobile on the mesothorax and an independent but concealed prepectus is present in Tiphidae and Sierolomorphidae. The prepectus is fused to the pronotum in Vespidae and to the mesepisternum in Pompilidae, Formicidae and some Scoliidae. The pronotum is mobile in Pompilidae and some Formicidae, and rigidly associated with the mesothorax in Vespidae, Scoliidae and some Formicidae (Gibson 1985). Scoliidae and Vespidae have a similar face, pterostigma and sunken prosternum, and may be closely related. Some similarities in the produced ventral angle of the pronotum and in the anterior expansion of the metapleuron suggest that the Formicidae, Scoliidae and Vespidae may be related. Sapygidae (parasites of Megachilidae), Sierolomorphidae and Bradynobaenidae are absent from Australia.

#### Key to the Families of Vespoidea Known in Australia

1. 1st (and sometimes also 2nd) metasomal segment node-like (i.e. strongly constricted anteriorly and posteriorly, medially enlarged, Figs 42.34, 36, 40); felt lines absent; posterolateral corner of mesosoma usually with opening of metapleural gland (Fig. 42.35); apterous worker caste present ..... **Formicidae** (p. 980)  
If 1st metasomal segment node-like then felt lines (Figs 42.32A, B) present; without apterous worker caste; opening of metapleural gland absent ..... 2
- 2(1). Wings absent or reduced to minute scales or apically expanded threads which lack closed cells ..... 3  
Wings well developed; fore wings with at least some closed cells ..... 6
- 3(2). Mesosoma without dorsal sutures (Fig. 42.32B); felt lines present ..... **Mutillidae** (♀♀) (p. 976)  
Mesosoma with transverse, dorsal sutures; felt lines absent ..... 4
- 4(3). Bases of mid coxae at least partially concealed by mesosternal lobes and each compound eye large, in diameter more than half the length of the head ..... 5  
Bases of mid coxae usually concealed by mesosternal lobes; if lobes absent, then each compound eye small, in diameter less than half the length of the head ..... **Pompilidae** (pt, p. 974)
- 5(4). Mid tibia spiny; posterior margin of pronotum mid-dorsally straight (Figs 42.32E, F, H); neither hind tibial spur modified into a calcar; wings absent ..... **Tiphidae** (pt, p. 977)  
Mid tibia not spiny; posterior margin of pronotum mid-dorsally weakly concave; one hind tibial spur modified into a calcar; wings present (Fig. 42.30i) ..... **Rhopalosomatidae** (p. 974)
- 6(2). Bases of hind coxae concealed by broad, metasternal plate (Fig. 42.32K); fore wing apically with area of close, parallel ridges and grooves ('pseudovenation', Fig. 42.32j). ..... **Scoliidae** (p. 978)  
Bases of hind coxae not concealed by broad, metasternal plate; fore wing without area of close, parallel ridges and grooves ..... 7
- 7(6). Pronotum acutely produced above tegula (Fig. 42.33); fore wing often folded longitudinally when at rest; lateral panel of pronotum ventrally acute; one hind tibial spur modified into a calcar ..... **Vespidae** (p. 979)  
Pronotum not acutely produced above tegula; fore wing not longitudinally folded; lateral panel of pronotum usually ventrally rounded, if more or less acute then hind tibia without calcar ..... 8
- 8(7). Bases of mid coxae partially concealed by mesosternal lobes (Fig. 42.32L) ..... **Tiphidae** (pt, p. 977)  
Bases of mid coxae not partially concealed by mesosternal lobes ..... 9
- 9(8). Lateral panel of pronotum ventrally rounded (Figs 42.30A, C-H); body rarely coarsely punctate; one hind tibial spur modified into a calcar; felt lines absent; mesopleuron with horizontal groove; inner margin of eye emarginate ..... **Pompilidae** (pt, p. 974)  
Lateral panel of pronotum ventrally acute (Fig. 42.32A); body coarsely punctate; neither hind tibial spur modified into a calcar; felt lines present on metasoma; mesopleuron without horizontal groove; inner margin of eye convex ..... **Mutillidae** (♂♂) (p. 976)

**57. Rhopalosomatidae** (Fig. 42.30i). Represented in Australia by *Olixon*, in which both sexes have reduced wings and a strongly modified mesosoma (Townes 1977a). Larvae feed ectoparasitically on Gryllidae (ORTH)

and spin a cocoon. Most non-Australian species are fully winged and superficially similar to nocturnal Ichneumonidae.

**58. Pompilidae** (Plates 5, T, 6, V; Figs 42.30A-H, 31).



Small to large (3.5–35 mm), legs usually long and slender with prominent tibial spurs. Inner margins of compound eyes at most weakly emarginate; pronotum freely articulating with mesothorax, mid-dorsally long, posterolaterally reaching tegulae, ventrally rounded; mid and hind coxae contiguous; tarsal claws toothed. Larvae with trilobed clypeus, distinct antennal papilla and vestigial 2nd thoracic spiracle. Cocoon present.

Pompilid behaviour is more uniform overall than that of Sphecidae or Vespidae, the other large families of predatory wasps. All pompilids are predators or parasites of spiders or of other pompilids. Females hunting for prey often walk or hop quickly with the wings flicking rapidly. Generally species are not highly prey-specific but tend to specialise on either web-forming, burrow-dwelling or errant spiders. There are no Australian records of cribellate spiders as prey. Scales on the bodies of some pompilids which specialise in orb-weaving spiders may enable the wasp to avoid entanglement in webs.

Pompilids provide each cell with a single spider, which is apparently a primitive habit among aculeates, and of necessity then each spider must be large relative to the wasp. Usually the prey is carried in the mandibles with the female wasp either walking backwards or making a hopping flight. Sometimes the legs of spiders are amputated for easier carriage and storage in the nest. Some species excavate or construct a cell before the prey is captured, others not until after. Nests may contain one or several cells. Ground nesting predominates. Females which dig in sandy soil have a well-developed rake of long spines on the fore tarsus. The rake spines are much shorter in species digging in harder soil, and absent in species which do not excavate a nest. Some pompilids paralyse spiders in their own retreats and oviposit on the spider *in situ*. In *Ferreola handschini* the spider is lightly paralysed and the wasp larva develops as an ectoparasite which finally kills the spider and pupates within the spider's retreat. *Ceropales* is parasitic, depositing its egg in the booklung of the prey of other pompilids before the spider is placed within the pompilid nest. Most Ageniellini construct mud nests, sometimes within the abandoned nests of other aculeates.

#### Key to the Subfamilies of Pompilidae Known in Australia

1. S7 more or less flattened, not medially carinate; fore femur usually greatly enlarged (Fig. 42.30A); eyes finely hairy in ♀♀; hind tibia without dorsoapical spines; S3 without transverse groove ..... EPIPOMPILINAE
- Without above combination of characters ..... 2
- 2(1). S3 of ♀♀ (and often of ♂♂) usually with sharp, transverse groove (Fig. 42.31D); mid and hind femora without subapical spine-like bristles in grooves or pits; apical tarsal segment of each leg ventrally with double row of preapical spines, or spines absent ..... PEPSINAE (most species)
- S3 without transverse groove, though sometimes with broad, wide impression; mid and hind femora usually with 1 or more dorsal, spine-like bristles set in grooves or pits (Fig. 42.31B); apical tarsal segment

of each leg ventrally with single row of preapical spines, or spines absent ..... 3

- 3(2). Spine-like bristles at apex of hind tibia rather long, irregular in length and spacing, splayed; 2nd discoidal cell of fore wing usually with a small pocket in inner, posterior corner ..... POMPILINAE
- Spine-like bristles at apex of hind tibia shorter, of rather uniform length; 2nd discoidal cell of fore wing without pocket ..... 4
- 4(3). Compound eyes distinctly emarginate (Fig. 42.30F); apical sternum of ♀♀ without conspicuous hairs; mesosoma and metasoma at least partially yellow to orange ..... CEROPALINAE
- Compound eyes not distinctly emarginate; apical sternum of ♀♀ with conspicuous erect hairs; mesosoma and metasoma black ... PEPSINAE (*Minagenia*)

EPIPOMPILINAE. The morphologically and behaviourally primitive *Epipompilus* (28 spp.; Fig. 42.30A) locates spiders, especially clubionid and sparassid females with egg sacs, under bark, paralyzes them and oviposits *in situ*. Wasp larvae feed on both spider and egg sac. The genus occurs in Australia, New Zealand and South America (Austin 1985; H. E. Evans 1972).

CEROPALINAE. The grey-coloured *Ceropales* (2 spp.; Fig. 42.30F) sometimes trails other pompilids. *Irenangelus* (2 spp.) is yellow to orange in colour and rather ichneumonid like.

PEPSINAE. Pepsini: The large (up to 35 mm), black and orange *Cryptocheilus* (7 spp.; Fig. 42.30D) and *Hemipepsis* (1 sp.) are formidable in appearance, *Cryptocheilus* being a common predator of Sparassidae and Lycosidae. *Priocnemis* (10 spp.) preys on Clubionidae. Australian '*Chirodamus*' are rather diverse in appearance. Modifications of the head in the *Maurillus* group of genera are associated with their attacking trap-door spiders and *Cteniziphantes* (2 spp.) is unusual in having 13-segmented antennae in the female. *Iridomimus* (2 spp.; Fig. 42.30B) is a brachypterous ant-mimic. Ageniellini (Fig. 42.30C): 1st metasomal segment anteriorly slender, giving a petiolate metasoma. *Auplopus* (6 spp.; Plate 6, V) nests in hollow twigs or abandoned nests of other aculeates, making cell walls of mud and closing the nest with mud and resin. The jugal lobe is absent in an undescribed genus (Fig. 42.30E). Psoropempulini: *Psoropempula* (11 spp.) combines morphological features of both Pepsinae and Pompilinae and possibly parasitises nests of other pompilids.

POMPILINAE. *Pompilus cinereus*, widely distributed through African, Indo-Oriental and Australian regions, is a common species of coastal dunes, sandy river beds and banks. *Ctenostegus* (65 spp.), predominantly grey and black with 2 submarginal cells in the fore wing, excavates simple nests in sandy soil and preys on errant spiders (Lycosidae, Pisauridae, Clubionidae). *Batozonellus* (2 spp.) and *Episyron* (5 spp.) specialise on orb weaving spiders. *Elaphrosyron* (1 sp.) and *Telostegus* (3 spp.) prey on Thomisidae. In *Idiaporina* (2 spp.; Fig. 42.30H) the wings are rather short and slender and some distal cells are lost from the fore wing. Several species of *Ferreola*, *Paracyphononyx*, *Turneromyia* (Plate 5, T; Fig. 42.30G)

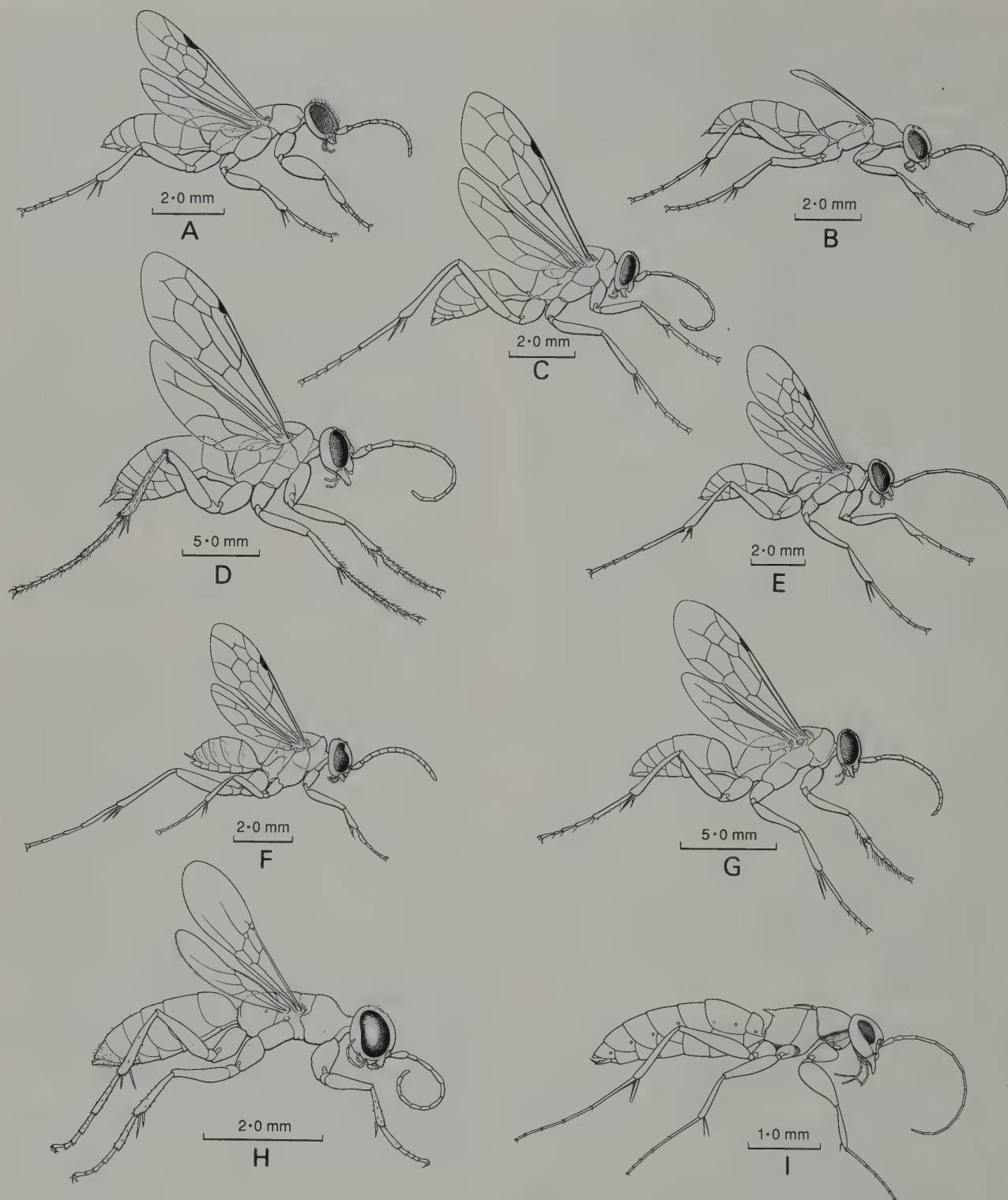


Fig. 42.30 Vespoidea: A, *Epipompilus* sp., Pompilidae-Epipompilinae; B, *Iridomimus* sp., Pompilidae-Pepsinae; C, *Phanagenia* sp., Pompilidae-Pepsinae; D, *Cryptocheilus* sp., Pompilidae-Pepsinae; E, unnamed Pompilidae-Pepsinae; F, *Ceropales* sp., Pompilidae-Ceropalinae; G, *Turneromyia* sp., Pompilidae-Pompilinae; H, *Idiaporina* sp., Pompilidae-Pompilinae; I, *Olixon* sp., Rhopalosomatidae, ♀. [A–G by T. Binder; H by T. Nolan; I by S. P. Kim]

and *Ctenostegus* form a mimicry complex of wasps with predominantly black to blue-black bodies combined with orange pronotum and sometimes head. The fore wing can be folded longitudinally in many Pompilinae. [Richards

and Hamm 1939; Townes 1957; H. E. Evans 1962–84; Wolf 1972; Harris 1987]

**59. Mutillidae** (Figs 42.43A, B). Heavily sclerotised, often metallic. Inner margins of compound eyes not



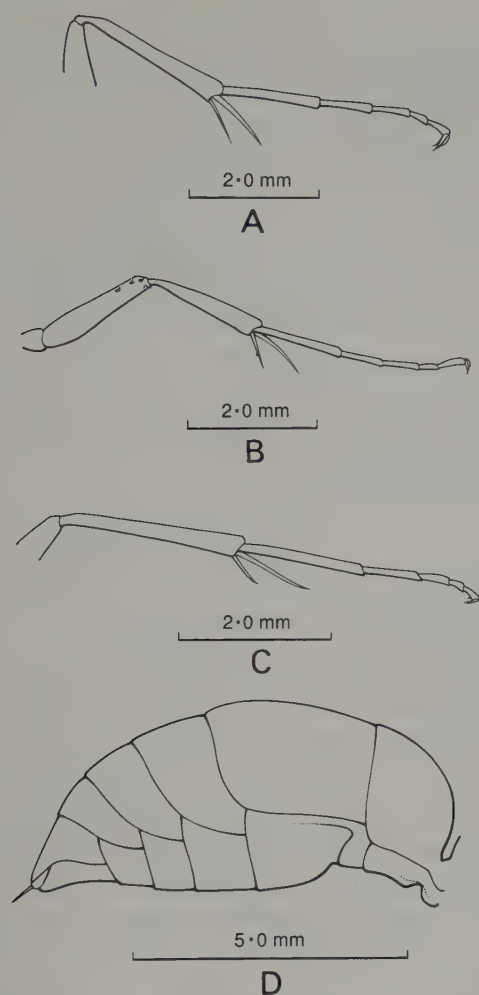


Fig. 42.31 Pompilidae: A, *Pompilus* sp., Pompilidae-Pompilinae, hind leg; B, *Pompilus* sp., mid leg; C, *Irenangelus* sp., Ceropalinae, hind leg; D, *Cryptocheilus* sp., Pepsinae, metasoma, lateral. [T. Nolan]

strongly emarginate; mid and hind coxae close together; T3 with felt lines (elongate hairy depressions associated with glands); stridulatory area sometimes exposed at base of T4. Males winged; fore wing without pseudovenation; hind wing with neither plical nor jugal lobes; pronotum with some freedom of movement on mesothorax, mid-dorsally short, posterolaterally reaching tegula. Females wingless, ant-like; mesosoma dorsally without transverse sutures; sometimes very small (length 3–23 mm). Larvae with 4-toothed mandibles and reduced 2nd pair of thoracic spiracles. Cocoon present. Females search on the ground (especially bare, sandy areas), tree trunks and walls for the nests of Sphecidae, Vespidae and Apoidea, which they parasitise. Males fly rapidly close to the ground and sometimes near smooth, sun-lit, tree trunks. Both sexes can be locally abundant in late afternoon. Males and females are rarely seen *in copula*. Larvae are usually solitary, although up to four individuals develop on a single host in a few species. Most Australian species are placed in the portmanteau genus '*Ephutomorpha*' but there are many undescribed, endemic genera, some show-

ing taxonomic affinities with South American genera. *Odontomutilla* (1 sp.) and *Timulla* (2 spp.), both restricted to northern Qld, are relatively recent incursions from the Afrotropical and Oriental regions. [André 1903; Brothers 1975]

**60. Tiphidae** (Plate 5, R; Figs 42.32C–I, L). Inner margins of compound eyes not strongly emarginate; pronotum freely articulating with mesothorax, mid-dorsally usually long, posterolaterally reaching tegula, ventrally rounded; mesosternum usually with plate-like extensions over mid coxae; propodeum not tripartite; fore wing without pseudovenation. Larvae with 4-toothed mandibles and 2nd pair of thoracic spiracles reduced or absent. Cocoon present. Most are presumed to parasitise scarab larvae (COLE) in the soil; the legs of females are stout and modified for digging.

#### Key to the Subfamilies of Tiphidae Known in Australia

1. Winged ..... 2  
Wingless (♀ only) ..... THYNNINAE
- 2(1). Antennae arising from simple sockets; mid tibia with 1 or 2 spurs ..... 3  
Antennae arising from beneath frontal ridge or lobe; mid tibia with 2 spurs ..... 4
- 3(2). Fore wing with 2 submarginal cells (Fig. 42.32C); mid tibia with 1 spur ..... TIPHINAE  
Fore wing with 3 submarginal cells (Fig. 42.32D); mid tibia with 2 spurs ..... ANTHOBOSCINAE
- 4(2). 1st submarginal cell of fore wing usually with spur-like cross-vein (Fig. 42.32G); if cross vein absent, 2nd submarginal cell receiving 2 recurrent veins (Fig. 42.32I) ..... THYNNINAE  
1st submarginal cell of fore wing without cross-vein; 2nd submarginal cell receiving 1 recurrent vein ..... MYZININAE

ANTHOBOSCINAE (*Anthobosca*, 30 spp.) are mostly black, 5–26 mm long and scoliid-like but lack the tripartite propodeum and pseudovenation (Fig. 42.32D). The subfamily has a principally Southern Hemisphere distribution and may be the sister group to the remainder of the Tiphidae. There is one 4–11 mm species of *Tiphia* (TIPHINAE) in northern Australia (Fig. 42.32C). MYZININAE (4 spp., 7–25 mm long) occur in W.A. and inland N.S.W. and Vic.; some non-Australian species parasitise tenebrionid larvae (COLE) in the ground.

THYNNINAE (715 spp.; Plate 5, R; Figs 42.32E–I). Small to large (2.2–40 mm), often brightly coloured; females wingless, ocelli usually absent, mid and hind tibiae with spiniform setae, mesosoma slender and divided by transverse sutures; males fully winged, usually larger than females. Diverse in and largely restricted to Australia and South America, which share no genera. Also represented in New Guinea, on some south-west Pacific islands and by a few species in the Oriental region. Adults are common in most regions in undergrowth and on flowers, in some cases being important pollinators. Females may produce a pheromone to attract males (Ridsdill-Smith 1970). Coupling is often prolonged with males carrying females to flowers where both feed on nectar. In some

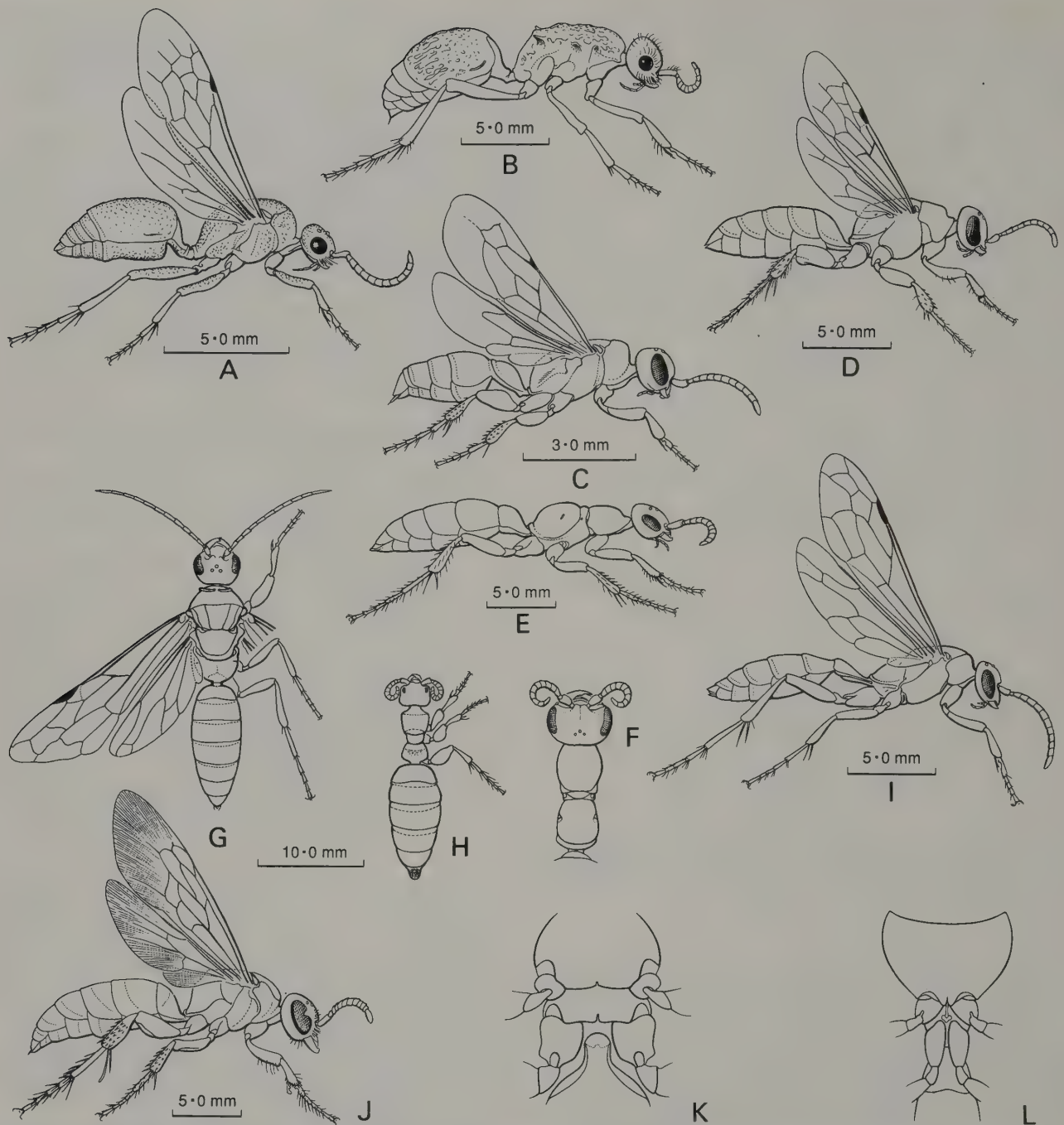


Fig. 42.32 Vespoidea: A, '*Ephutomorpha*' sp., Mutillidae, ♂; B, *Bothriomutilla rugicollis*, Mutillidae, ♀; C, *Tiphia* sp., Tiphidae-Tiphiinae; D, *Anthobosca* sp., Tiphidae-Anthoboscinae; E, *Diamma bicolor*, Tiphidae-Thynninae, ♀; F, same, dorsal; G, *Hemithynnus* sp., Tiphidae-Thynninae, ♂; H, same, ♀; I, *D. bicolor*, ♂; J, *Campsomeris* sp., Scoliidae; K, Scoliidae, mesosoma, ventral; L, Tiphidae, mesosoma, ventral, ♂. [A–J by T. Binder; K, L by A. Hastings]

genera males feed females by regurgitation or from a droplet retained in a hair-fringed, ventral excavation of the head. Flowers of some orchids mimic female thynnines and are pollinated as male thynnines attempt copulation (pseudocopulation, see p. 85). The female of *Diamma* (Plate 5, R; Figs 42.32E, F) is unique among Australian Thynninae in that it is metallic purple or green, has ocelli, is larger than the male (Fig. 42.32I) and parasitises mole crickets. [Given 1954 a,b; Salter 1967]

Brachycistidinae and Methochinae, both of which have

wingless females, are absent from Australia (Königsmann 1978b; G. R. Brown 1985; Rasnitsyn 1986).

**61. Scoliidae** (Figs 42.32J, K). Mostly large (9–36 mm), stout bodied, densely hairy and extensively modified for fossorial habit. Larvae with 3-toothed mandibles. Cocoon present. All Australian species belong to the SCOLIINAE: inner margins of compound eyes strongly emarginate; pronotum closely co-adapted to mesothorax, not moving freely on it, mid-dorsally short, posterolaterally reaching to tegula, ventrally acute; meso- and metathoracic sterna



flattened, metasternum plate-like and overlapping hind coxae, mid and hind coxae widely separated; propodeum tripartite; mid femur without trochantellus; mid and hind tibiae with strong spines; tarsal claws simple; fore wing apically with close, radiating ridges and grooves ('pseudovenation', cf. Blattodea) and true venation not reaching wing apex. In the Palearctic Proscoliniinae (*Proscolia* only) the inner margins of the compound eyes are very weakly emarginate and the mid tibia has 2 spurs. Superficially similar to Anthoboscinae (Tiphidae) which are also fossorial parasites of scarab larvae. Females dig into soil or wood where they paralyse coleopterous larvae and deposit an egg transversely. Several Australian species parasitise larvae of scarab pests of sugar cane. Metasoma extensively orange-yellow in *Campsomeris* and *Pseudotrielis*. *Scolia* and *Austrelis* predominantly black. *Trisciloa ferruginea* is one of the largest Australian wasps. [Betrem 1928, 1933; Day *et al.* 1981]

**62. Vespidae** (Plate 6, K, N, T; Fig. 42.33). Mostly large (5–32 mm). Inner margins of compound eyes strongly emarginate except in Masarinae; mandibles generally short and broad but becoming elongate and crossing to form a distinct 'X' in many Eumeninae; glossae and paraglossae sometimes greatly produced (Fig. 42.33B) and with apical, sclerotised pads (*acroglossal buttons*); pronotum not freely movable against mesothorax, mid-dorsally short, posterolateral corner acutely produced dorsal to tegula and spiracle cover lobe close to tegula (remote in Stenogastrinae); *parategula* (an apically rounded, more or less dorsoventrally flattened lobe arising from posterolateral corner of mesoscutum and lying adjacent to the tegula) present in Eumeninae and some Masarinae; calcar of hind tibia apically curved, bifid or trifid in some Masarinae, strigil well developed; fore wing at rest folded longitudinally in all except Stenogastrinae, Euparagiinae and many Masarinae; primitively with 3 submarginal cells in fore wing; cell 1M of fore wing elongate; hind wing jugal lobe often present; primitively in aculeates and vespids the terga overlap sterna and are freely movable against them—this is the case in Euparagiinae and many Masarinae—varying degrees of fusion occur within other Vespidae culminating in complete obliteration of sutures between some terga and sterna (e.g. in *Ropalidia*); posterior metasomal segments often retractile within segment 2; T3 and S3 often enlarged; females oviposit into cells before provisioning. Larvae variable, usually spinning a cocoon. Eusocial behaviour evolved probably once, in the Stenogastrinae + Polistinae + Vespinae. Several of the subfamilies are sometimes accorded family rank. Probably the Stenogastrinae, Polistinae and Vespinae form a monophyletic assemblage whose sister group is the Eumeninae. Euparagiinae and Masarinae appear to have diverged independently from the base of the vespid lineage (J. M. Carpenter 1988).

In Stenogastrinae, from the Oriental region and New Guinea, T2 and S2 are fused into a long, slender petiole and the fore wing is unfolded. They are either subsocial or eusocial; prey are masticated and larvae are fed progressively.

The Euparagiinae are a small, Nearctic group of solitary, ground-nesting predators of weevil larvae.

#### Key to the Subfamilies of Vespidae Known in Australia

1. Fore wing at rest not longitudinally folded, with 2 submarginal cells (Fig. 42.33A); trochantellus absent ..... MASARINAE
- Fore wing at rest longitudinally folded, with 3 submarginal cells (Figs 42.33C–I); mid leg with trochantellus ..... 2
- 2(1). Tarsal claws bifid; parategula present; not social ..... EUMENINAE
- Tarsal claws simple; parategula absent; social ..... 3
- 3(2). Hind wing with anal lobe; hind coxa without posterodorsal, longitudinal carina ..... POLISTINAE
- Hind wing without anal lobe; hind coxa with posterodorsal, longitudinal carina ..... VESPINAE

EUMENINAE (300 spp.) are mostly solitary, nesting either in the soil, in pre-existing cavities (such as beetle tunnels in wood or abandoned mud nests of other Hymenoptera), or in free mud nests which they build themselves. *Ischnocoelia*, nesting in cavities in wood, constructs cells of chewed leaves pasted together with resinous secretion, but mud is the usual nest material. Often nest entrances are surmounted by fragile mud turrets which may exclude parasites or dust. Females provision cells with caterpillars, although some non-Australian species utilise sawfly or beetle larvae. Eumenines are common around standing water in inland Australia, and the larger species of *Delta* and *Abispa* were followed by Aborigines seeking water. Of the approximately 30 genera present in Australia about a dozen are endemic and most of the rest are represented in Oriental and south-west Pacific regions.

Two mid tibial spurs are retained in several genera. *Australozethus* (3 spp.; Plate 6, N) from the south-east, south-west and Lord Howe I. lacks a jugal lobe in the hind wing. In *Macroclymma* (2 spp.), from coastal regions in the east and south-west, the posterior extremity of the enormous tegula reaches slightly behind the posterior margin of the mesoscutellum. *Ischnocoelia* (10 spp.; widespread, including inland areas) and *Elimus* (2 spp.) have a very elongate, slender T1 whereas in *Deuterodiscoelius* (7 spp.; Fig. 42.33C; predominantly moister areas of east and west) and *Pachycoelius* (3 spp.) T2 has a slender anterior portion and an abruptly expanded posterior portion.

In all other eumenine genera there is only a single mid tibial spur. In the metallic green *Eudiscoelius* (1 sp.; T2 with transverse, anterior carina) and *Eumenes* (2 spp.; T2 without carina, posterior margin of T3 differentiated step-like from the rest of the tergum) T2 is very slender and the mandibles are long. Both genera are more diverse in the Oriental region. *Delta* (9 spp.; Fig. 42.33H) comprises mostly large (up to 30 mm long) species in which T2 is long and slender and T3 lacks a step-like posterior margin. The jug-like nests of several black and orange species are common on buildings throughout Australia. The 4 spp. of *Abispa* (Fig. 42.33F) are all very large



(22–32 mm), stout bodied, have a trituberculate metanotum and build massive mud nests, sometimes in buildings. In *Rhynchium* (7 spp.; northern areas) the mesoscutellum is impunctate. In *Acarozumia* (3 spp.; Fig. 42.33G) and *Acarodynerus* (17 spp.) the propodeum and sometimes also the metasomal terga and sterna have pouches in which shelter the dispersing stages (hypopi) of symbiotic saptroglyphid mites. *Paralastor* (130 spp.; widespread), in which the 2nd submarginal cell of the fore wing is petiolate (Plate 6, T; Figs 42.33D, E), and several smaller genera in which the submarginal cell is sessile include the majority of eumenines in the 5–15 mm size range. *Subancistrocerus* (1 sp.) has a pair of transverse carinae on T2.

In some Eumeninae the mandibles are elongate and decussate. Females sometimes have one or two pits (cephalic foveae) on the vertex; probably these are the openings of pheromone glands. The apical flagellar segment of males usually is specialised and with the preapical segments forms a hook which curls around the female antenna during mating. [Cardale 1985; Carpenter and Cumming 1985]

MASARINAE (33 spp.) are solitary, and bee-like in that they provision their larval cells with pollen and nectar. Adults frequent flowers (e.g. *Eucalyptus*, *Melaleuca*, *Hakea*, *Leptospermum*, *Goodenia*) and water, and may be locally abundant. Both genera are endemic and more common in arid regions. *Paragia* (27 spp.; Fig. 42.33A) nests in hard, clay or sandy soils, with the entrance sometimes surmounted by a mud turret. *Metaparagia*, nesting in sandy ground, does not build turrets. Some non-Australian masarines construct mud nests attached to trees and shrubs. Specialised setae on the gena and mandibles of one species of *Metaparagia* form a basket (psammophore), presumably to transport sand particles excavated from the nest. [Houston 1984; Cardale 1985; Snelling 1986]

POLISTINAE (34 spp.) are eusocial. Colonies are founded by one or more queens, sometimes in the company of a swarm of workers. If there are several foundress queens either egg-laying has been suppressed in all but one by the time the first daughter workers emerge, or some sort of serial polygyny generally ensues. Some non-Australian Polistinae form large, multi-queened colonies. Queens and workers are usually morphologically similar, differing only in behaviour and ovary development. Adults are nectar feeding and prey principally on caterpillars which are masticated and fed progressively to the larvae. At night adults rest on the upper surfaces of nests or close by. Colonies may be perennial in warmer regions but die out in cooler areas where inseminated queens overwinter on top of the old nest.

The paper nests are constructed from carton, a pulp of macerated plant fibre and oral fluids. Nests consist of single or multi-tiered combs suspended by one or more peduncles in sheltered positions or concealed in cavities in wood or in the ground. The combs are either vertical or horizontal, occasionally spiralling from one tier to the next, and may be enclosed by a paper envelope. *Ropalidia plebeiana* forms massive aggregations of nests

under rock overhangs and bridges in the south-east. The combs of *Ropalidia kurandae* are concealed by leaves glued together. *Ropalidia* (22 spp.), in which T3 and S3 are often fused, and *Polistes* (12 spp.; Fig. 42.33i) are more numerous in warmer, moister regions of the north and east. They are beneficial in destroying numbers of pest caterpillars but often nest under the eaves of houses where they can be a nuisance because of their painful stings. [Cardale 1985]

The VESPINAE (2 spp.) are represented by accidentally introduced species of the Holarctic genus *Vespula*. *Vespula germanica* is a widespread pest in southern Australia whereas *V. vulgaris*, restricted to Vic., is of lesser importance. Both are eusocial with an egg-laying queen and many thousands of smaller, sterile workers to each mature colony. Colonies are founded by a single queen in pre-existing cavities in the ground, in trees or in buildings, and nests consist of a paper comb and envelope. To collect carbohydrates and protein, wasps forage on blossoms, fruit and carcasses and prey on other insects (including flies and honey bees). Food is masticated and fed progressively to larvae. The predominantly Holarctic and Oriental genus *Vespa* is present in New Guinea. [Cardale 1985; J. M. Carpenter 1987]

**63. Formicidae** (by R. W. TAYLOR). The ants are a group of uncertain (but probably vespoid) affinity, and consist of eusocial species in which the worker caste is permanently wingless. A few species are secondarily workerless, with parasitic reproductive females inquiline in the nests of other ants. In most species the reproductive females (queens) are winged at emergence, but the wings are always shed later in life after mating. Males are permanently winged. Exceptions include species with apterous and variously worker-like reproductive females or males. All forms have a nodiform, scale-like or binodal 'waist' behind the articular constriction separating the propodeum and metasoma. This comprises either the modified true abdominal segment 2 (the 'petiole') (Figs 42.40B, C, G, H), or segments 2 and 3 (the latter in this case is the 'postpetiole') (Figs 42.40A, E, F, I, K, L, N). The terminal, large section of the metasoma (beginning with abdominal segment 3 or 4, depending on the composition of the waist) is the 'gaster'. The term 'metasoma' is seldom used in myrmecology and the mesosoma is often called the 'trunk' or 'alitrunk' (Fig. 42.34). Most ants have a pair of large metapleural glands, each with a sclerotic bulla, opening through a small orifice in the lower, posterolateral corner of the mesosoma (Fig. 42.35). Exceptions (probably due to secondary loss) include the males of some groups (e.g. some *Myrmecia*, *Aenictus*), and all forms of the formicine genera *Oecophylla*, *Polyrhachis* and (Australian and most other) *Camponotus*. Metapleural glands or their homologues are unknown elsewhere in the Hymenoptera.

Internally adult ants are remarkable chiefly for (1) the development of the crop—especially of its sclerotic posterior valve, the proventriculus, which is elaborate in the Dolichoderinae and Formicinae, and varies widely to furnish tribal or even generic characters; and (2) the great variety and prominence of glands which open externally



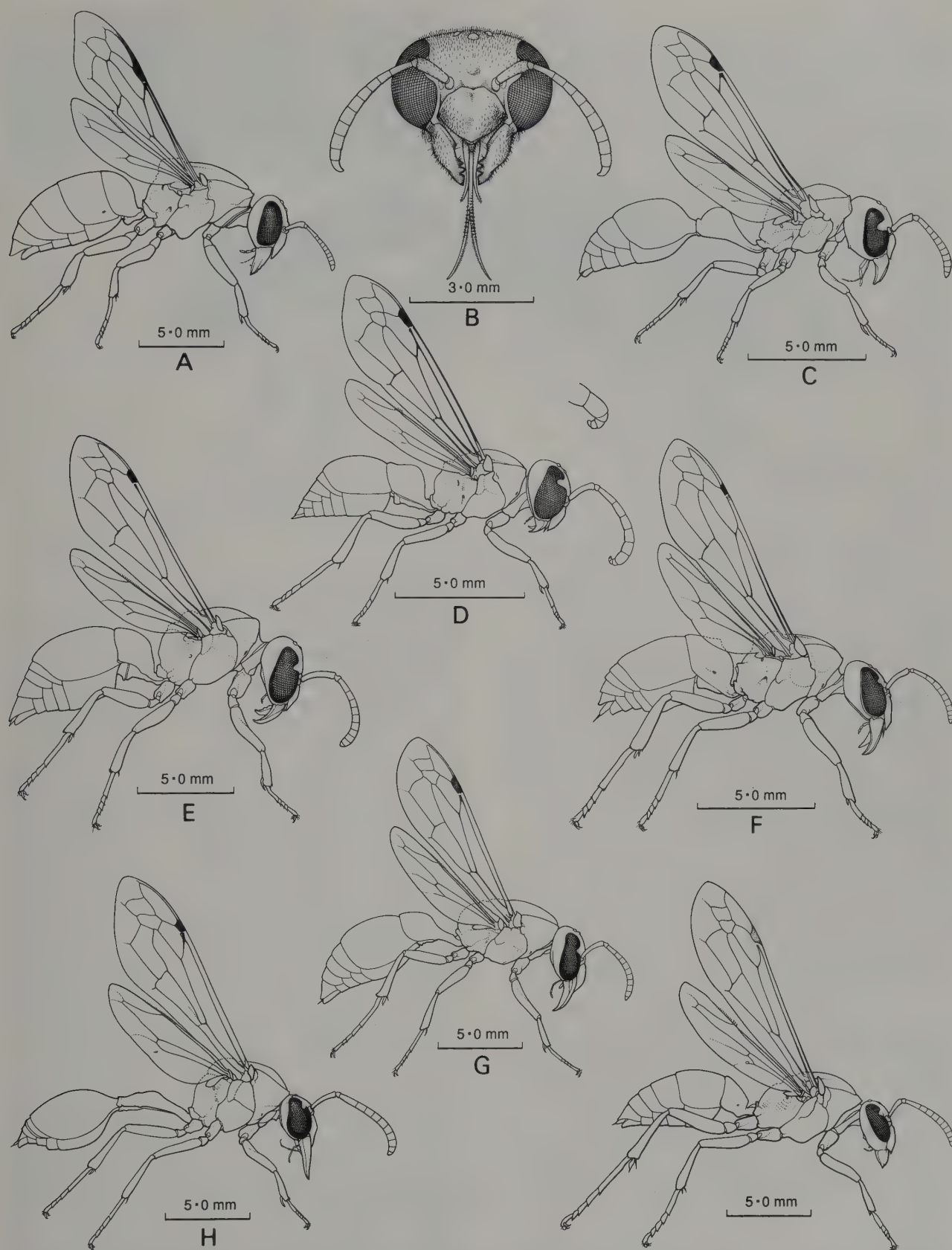


Fig. 42.33 Vespidae: A, *Paragia* sp., Masarinae; B, *Rolandia* sp., Masarinae, head, frontal; C, *Deuterodiscoelius* sp., Eumeninae; D, *Paralastor* sp., Eumeninae, ♂; E, *Paralastor* sp., ♀; F, *Abispa* sp., Eumeninae; G, *Acarozumia amaliae*, Eumeninae; H, *Delta* sp., Eumeninae; I, *Polistes* sp., Polistinae.

[T. Nolan]

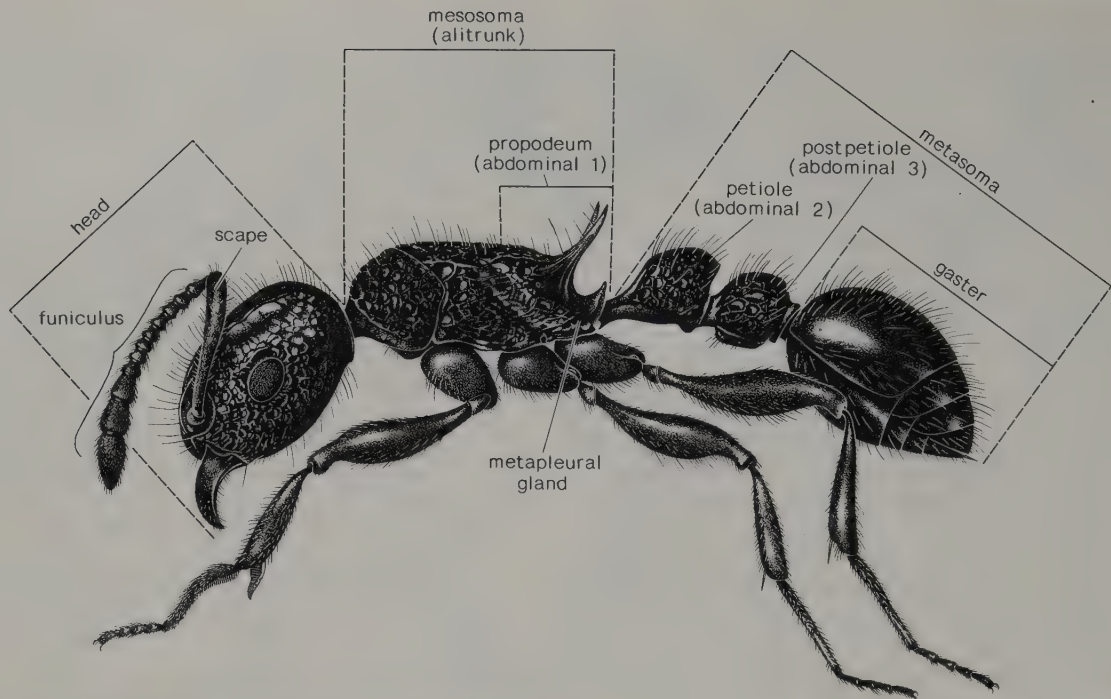


Fig. 42.34 *Tetramorium pacificum*, Formicidae-Myrmicinae, worker, lateral view.

[F. Nanninga]

on various parts of the body, many of them secreting pheromones, which function in social and sexual communication.

The ants of common experience are foraging workers. They have a characteristic facies, and are normally confused (among non-mimics) only with female mutillid or thynnine wasps or other wingless Hymenoptera, all of which lack the peculiar ant waist and metapleural glands. There are perhaps 20 000 species of ants world-wide, many of which are undescribed. Only about a quarter of the Australian fauna has been named.

The female castes are the female proper or *queen* (Figs 42.40i, j), and the *worker*. The worker caste is sometimes subdivided into *major* (= *soldier*), *media*, *minor*, etc. phases or subcastes (Figs 42.40L–O). Female caste differences are phenotypic, and arise during development in response to variation in the amount and composition of the larval food, pheromones or nutrient stored in the egg. The female antennae are elbowed, with an elongate scape (Fig. 42.34). The sting is present and functional in many species (Figs 42.40A–F), but largely vestigial in Dolichoderinae and Formicinae (Figs 42.40G, H), where the venom is spread or sprayed from the modified gastral apex. The virgin queen usually bears wings, has a well-developed pterothorax and flight muscles, large compound eyes and 3 ocelli; she is usually larger than workers of the same species, with a relatively bulky gaster containing well-developed ovaries and fat body.

In keeping with their aptery worker ants have greatly reduced mesosomal structure. The only flexible or semi-flexible joint lies between the prothorax and the mesothorax, and even this is fused in Myrmicinae, many Ponerinae, and some genera of other subfamilies. The metanotum may be obsolete, represented by a narrow

impressed piece with paired spiracles (*Myrmecia*, some Formicinae) or by a transverse metanotal groove. Cephalic features are as in the queen, but usually with smaller (sometimes minute or absent) eyes, and ocelli reduced or lacking; mouth-parts, antennae and sting are usually the same, and function similarly in both worker and queen. Soldiers, when present, are larger than other workers and have disproportionately large heads, sometimes absolutely larger even than in the queen. Worker minor and soldier may be connected by a series of inter-gradient forms (*Anisopheidole*, *Pheidologeton*, most *Camponotus* and *Melophorus*), or are normally without intermediates (exhibiting dimorphism, as in *Pheidole* (Figs 42.40L–O) and *Oligomyrmex*). The evolution of caste in worker ants is far more spectacular than in other Hymenoptera, perhaps because it has not been restrained by aerodynamic considerations which apply to flying wasps and bees, which rarely have morphologically distinguishable worker phases.

Male ants usually bear non-deciduous wings, and have relatively small heads, large compound eyes and ocelli, and less-distinctly elbowed antennae; their mandibles are often much modified or very reduced (Fig. 42.40K). In most species males are larger than workers but smaller than queens. Male genitalia are often unremarkable, but appear promising for taxonomic discrimination of some otherwise similar species in *Myrmecia* and *Amblyopone*, and the genera of Dolichoderinae. A few regional species have (sometimes remarkably) worker-like ergatoid males, which sometimes coexist with normal winged males (some *Hypoponera*, *Cardiocondyla* and *Technomyrmex*).

The primitive number of palp segments in both sexes of ants is maxillary 6, labial 4, but this formula may be reduced to as low as 1-1 in some specialised genera. The



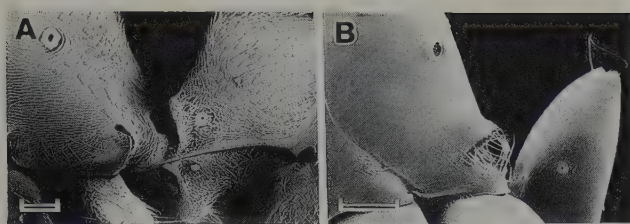


Fig. 42.35 Metapleural gland openings of ant workers: A, *Amblyopone* sp., Ponerinae; B, *Prolasius* sp., Formicinae. Scales = 0.1 mm.

[C. Beaton]

primitive antennal count is 13 in the male and 12 in the female, and this number may be reduced in both sexes. Some queens and workers of the myrmicine tribe Dacetini have only 4-segmented antennae, but male numbers do not fall so low. Ant wing venation has undergone convergent reduction in many lineages in different subfamilies, and this is often related to small body size. Even primitive ants, such as those of genus *Amblyopone*, may have the wing venation very reduced in small species. Reversal of the size trend does not lead to replacement of regular venational elements. In members of the 'poneroid complex' of subfamilies (Myrmecinae, Pseudomyrmecinae, Ponerinae, Myrmicinae, Dorylinae and Leptanillinae, in Australia) abdominal segment 4 is said to be 'tubulate'. Its tergum and sternum are aligned laterally and partially or completely fused to form a tubular structure, a portion of which is inserted into the exoskeleton of the preceding segment and articulated there to facilitate free movement of the sting-bearing gastral apex (Figs 42.40B, C). In many species this tubulate structure is strongly constricted, so that its anterior portion forms a small ball joint enclosed in the posteriorly constricted segment 3 exoskeleton (Figs 42.34, 40A, E, F). This results in the formation of a postpetiole (from segment 3), a configuration for which segment 4 tubulation is a necessary precursor. In the less-derived, non-tubulate segment 4 of the 'formicoid' subfamilies (Nothomyrmecinae, Dolichoderinae and Formicinae) the sclerites are not fused laterally or modified to assemble a tubular structure, and there is no postpetiole (Figs 42.36, 40G, H). The gaster of *Sphinctomyrmex* (Ponerinae: Cera-pachyini) (Fig. 42.40D) is unique, because abdominal segments 4, 5 and 6 are serially tubulate. If abdominal tubulation is homologous in the various groups which show it, the poneroid complex could represent a major lineage of ant evolution, derived from an ancestor probably not unlike the primitive Australian genus *Nothomyrmecia* (Fig. 42.36).

Ant colonies are perennial. They typically include a single queen supported by a force of workers, which may number from a few to many thousands, depending on the species and age of the colony. Brood is usually present, and may include eggs, larvae and pupae. Its composition varies seasonally, but all stages are normally found in the spring and early summer. In a few species brood is lacking in winter colonies (some *Myrmecia*, perhaps all *Sphinctomyrmex*), but most overwinter partly-grown larvae, sometimes in diapause. Virgin queens and males

are produced, usually annually, by mature colonies and released at a season and time of day fixed for the species, in order to participate in a massed nuptial flight or flights with sexuals from other colonies. The exact timing of this activity is synchronised regionally by weather-related cues. In a few cases winged sexuals are produced in late summer and overwintered before release. Females seem often to mate only once, and when inseminated they leave the swarms and soon divest themselves of their wings to become 'de-alate' (a process termed 'allectomy' or 'de-alation'). They then secrete themselves alone or in small groups in a suitable place and begin to lay the eggs which will later produce the first workers of a founding colony. Colony founding by co-operating queens is termed 'pleometrosis'; by a single queen 'haplometrosis'. Males disperse to die after mating. The sperm acquired at mating by queens is stored in their spermathecae, and used for fertilisation of eggs, in many cases laid years after the death of donor males.

In the higher ants the wing muscles of foundress queens are converted into fat body to serve as a nutritional reserve. Many such species do not leave the small chamber of the initial nest to forage, but feed the growing larvae with 'trophic' or food eggs. This conversion of female substance into food for offspring can be likened to milk-feeding in mammals. In some more primitive genera (and others) the founding queens leave the nest chamber to forage for prey with which to feed the larvae. This activity seems always to cease about the time the first workers appear in the new colony, to take over the work of foraging. The founding queens of a Japanese species of *Amblyopone* are known to wound the larvae (nonlethally) in order to obtain haemolymph for nourishment, and the larvae of *Leptanilla* have special organs for provision of haemolymph to adults.

In many Australian ants the queens are secondarily worker-like ergatoids ('ergatogynes'), which do not develop wings, and have reduced mesosomal structure,

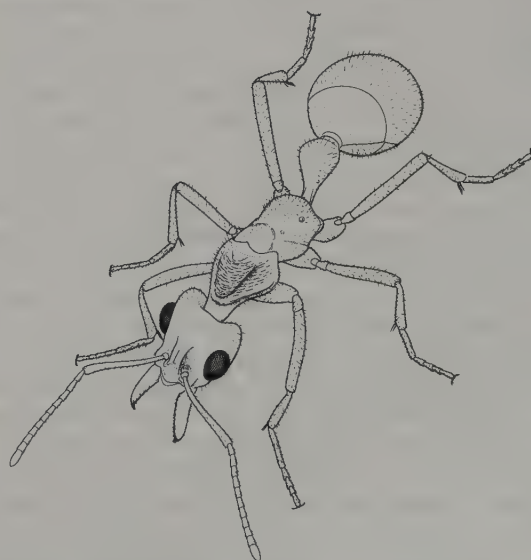


Fig. 42.36 *Nothomyrmecia macrops*, Formicidae-Nothomyrmecinae; worker in alert posture.

[S. P. Kim]





Fig. 42.37 Larval mouth-parts, showing labrum, mandibles and labium; *Nothomyrmecia macrops*, Formicidae-Nothomyrmecinae. Scale = 0.01 mm. [C. Beaton]

sometimes different from that of conspecific workers. These are found in some *Myrmecia*, *Heteroponera* and *Mayriella* species, and in most, or all, *Leptogenys*, *Sphinctomyrmex* and *Leptomyrmex*. In many species of *Rhytidoponera*, *Diacamma* and *Bothroponera* neither queen nor differentiated ergatogyne is known, and the queen function is assumed by fertilised workers or 'gamergates' which are capable of mating and thus of diploid egg production. In some *Rhytidoponera* species several such workers appear to replace the dead primary queen as secondary reproductives, but in most others true queens are unknown and probably absent. Ergatogynes and gamergates frequently seek mates in a precopulatory promenade on the nest surface or surrounding soil or vegetation, and may attract conspecific males by pheromonal 'sexual calling'. In some genera, such as *Onychomyrmex*, *Aenictus* and *Leptanilla*, which follow the nomadic and group-predatory existence typical of 'army ants', the reproductive female is a bizarre type of blind ergatogyne with a periodically enlarged, ovary-filled gaster, and is referred to as a 'dichthadiigyne'. In these and some other species with flightless reproductive females mating apparently occurs in the nests with males which have joined from other colonies, and new colonies are produced by fission, involving swarming on foot, or 'hesmosis'. Newly mated queens of a few ant species enter the nests of another species to live there as social parasites, or inquilines. In 'temporary social parasites' the host queen is promptly killed by the inquiline, or by her own alienated workers, and a mixed colony is formed of host workers and the offspring of the inquilinous queen. This gradually develops into an independent colony of the inquilinous species as the host workers die. In Australia *Rhoptromyrmex* and some *Myrmecia* and *Bothriomyrmex* are likely examples. The queens of 'permanent social parasites' live continuously with their host species, and commonly lack a worker caste altogether. Their males

probably move between host colonies to mate with virgin females. Australian examples include *Myrmecia inquilina* (hosts *M. nigriceps* and *M. vindex*) and *Strumigenys xenos* (host *S. perplexa*). The special type of permanent parasitism known as 'dulosis' or slave-making, where 'slave' workers are constantly replenished by the addition of pupae raided from the nests of the host species, is not known to occur in Australia.

Established colonies of ants may contain a single queen, or several might normally be present. The former condition is probably more usual, and in species where colonies are founded by pleometrosis the number of queens is often reduced to one through aggression or intervention by workers once they appear.

The eggs of ants are sometimes adhesive and clumped, which apparently aids manipulation by workers. Larvae have very reduced mouth-parts and share the white, grub-like apodous condition of other aculeates (Figs 42.37, 38). They depend on the queen (initially) and workers as food providers. Specialised hairs or tubercles which fasten the larvae to the nest walls or ceiling, or clump them together, sometimes attached to pupal cocoons, for quick transport by workers, are convergently developed in several lineages. The number of larval instars is not certainly known for any species, but there are likely 3. Last instar larvae of *Nothomyrmecia*, *Myrmecia* and most ponerines, and those of many formicines, spin a pupal cocoon, but the pupae are naked in Pseudomyrmecinae, Myrmicinae and Dolichoderinae, and some members of other subfamilies. Mature larvae are frequently banked with soil by workers prior to cocoon spinning. Cocoons are normally yellow or light-brown, and have a dark terminal spot, the meconium, formed by faecal material, which is not discharged by larvae until just before pupation. After emergence all solid waste produced by each larva, the cocoon, meconium and enclosed larval exuviae, is removed from the nest by workers, in a single package, or deposited with other solid wastes in a midden gallery within the nest. In some species brood may be deployed above ground in winter sunshine (*Dolichoderus* spp.), or on cool summer nights (some *Myrmecia* spp.), and some *Rhytidoponera* have dark brown or black cocoons, which are at times laid in the sun, apparently to capture radiant energy.

Most ant colonies live in more or less long-term nests

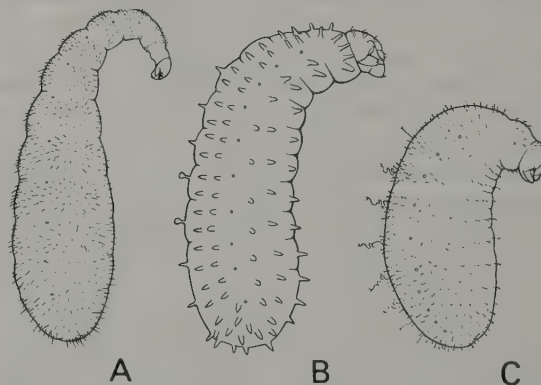


Fig. 42.38 Larvae of ants: A, *Amblyopone* sp., Ponerinae; B, *Hypoponera* sp., Ponerinae; C, *Pheidole* sp., Myrmicinae. [S. Monteith]



excavated in the soil or in (usually rotting) wood, or in pre-existing cavities in plants or rocks. Ant nests are unusual among those of social Hymenoptera, in that the brood is housed together in a single, continuous chamber. Separate individual brood cells, like those of wasps and almost all eusocial bees, are never constructed. The great majority of Australian species inhabit the ground layers, in chambers deep in the soil or under rocks or other objects. Here seasonal and daily fluctuations of moisture and temperature are buffered, in part by the movement of brood by workers, within the nest. Some species, particularly in arid areas, construct mound or disc nests, often with large entrance holes, and sometimes with a surface cover of pebbles, charcoal etc. Virtually the whole range of terrestrial nest types may be observed among the species of some larger genera (*Myrmecia*, *Rhytidoponera*, *Iridomyrmex* and *Camponotus*), but most genera are more restricted in nesting habits. In forested areas decaying logs and smaller pieces of rotting wood, including tiny twigs, gum nuts etc., may be utilised under favourable circumstances, but their inhabitants often move deep into the soil during dry conditions. Because of this ants can seem virtually to be lacking at times, even in northern rainforests. Although a number of Australian ants nest in twigs on standing vegetation (*Tetraponera*, *Metapone*, *Crematogaster*, *Myrmecorhynchus* and *Camponotus*) this habit is best developed in northern areas, especially in mangroves, and seems to be less common than in other parts of the world. Other tree-dwelling ants belong to *Podomyrma*, which frequently chooses crevices or beetle burrows in solid wood, to *Myrmecia mjobergi*, which builds in rainforest canopy epiphytic ferns, and to several *Iridomyrmex* and *Pheidole* species which live in pre-formed cavities of the epiphytic 'ant-house plants' *Myrmecodia* (Fig. 3.16) and *Hydnophytum*. Other symbiotic relationships are known between ants and plants of the Indo-Malayan intrusive flora of the north (see pp. 83–4). Various formicines use larval silk in nest construction, and this habit may be correlated with the absence of pupal cocoons in these groups. Arboreal *Polyrhachis* species, for example, often build nests of silk and plant fibres on leaves, twigs or bark, and even some soil-nesting species of the genus line their nests with silk. The tropical green weaver ant, *Oecophylla smaragdina*, builds nests of leaves drawn together by chains of workers, and secured with silk deposited by worker-manipulated larvae (Fig. 42.47). The colonies of various *Leptogenys* and *Diacamma* species move regularly, nesting in loose surface bivouacs. Those of the doryline and amblyoponine army ants, *Aenictus* and *Onychomyrmex*, use either temporary bivouacs or sheltered, more stable nests, in alternating 'nomadic' and 'statory' phases of migratory behaviour, which are related to regular cycles of brood production and development by their colonies. Two Australian *Polyrhachis* species are known to nest in the mud of mangrove flats subject to tidal flooding.

Adult ants are liquid-feeders. Some drink the haemolymph of prey animals, and most forage for carbohydrate-rich exudates of plants (sometimes taken from extra-floral nectaries) or secretions produced by sap-feeding hem-

ipterous insects. The mouth-parts, especially the buccal pouch, and the proventriculus remove almost all particulate material from liquids ingested by adult ants; adults of some species lack a peritrophic membrane. Most ant larvae eat solid food but in Formicinae and Dolichoderinae larvae predominantly use liquid food which probably is secondary. In some species, notably in harvesting ants, the larvae process solid food, and produce liquid secretions to nourish the adults. Some formicine and dolichoderine genera (*Leptomyrmex*, *Melophorus*, *Plagiolepis* and *Camponotus*), especially in arid areas, store honeydew and nectar in the enormously distended crops of special 'repletes' or 'honeypot' workers, which remain in the nests, and are provisioned by regurgitating foragers. Many genera of ants directly attend, and even protect or shelter hemipterous insects for their honeydew. Some formicines, notably in *Acropyga* and *Pseudolasius*, attend root-feeding pseudococcid Hemiptera within their nests. *Acropyga* virgin queens each carry a gravid female pseudococcid from the parent nest in their jaws throughout the mating flight, apparently in order to stock their foundation colonies with the necessary pseudococcids.

The booty of carnivorous, predatory or scavenging ants may include a wide range of arthropods, especially in primitive species. Many primitive species are unable to dismember prey, which is returned whole to the nest by individual foragers, or sometimes by group-retrieval. Fragments of larger prey organisms may be gathered by species capable of prey dissection, some of which (e.g. the 'meat ants' of the *Iridomyrmex purpureus* group) can quickly strip the skeletons of small dead vertebrates.

There are many peculiar adaptations related to foraging in ants. Some dacetines, for example, smear themselves with dirt while foraging, perhaps for camouflage, and many have an elaborate jaw-trap mechanism. The elongate, apically toothed mandibles are held widely apart under muscular tension by the labrum, which is raised between their bases. When long, anteriorly directed, labral sensory hairs touch potential prey the labrum is dropped to trip the violent jaw-snap. Highly specific predators include some *Amblyopone* and *Onychomyrmex* species on geophilid centipedes, *Cerapachys* and *Sphinctomyrmex* on other ants, *Discothyrea* on arthropod eggs, some *Leptogenys* on slaters, *Metapone* on termites, and most *Strumigenys* on Collembola. Some species of Myrmicinae and Formicinae, notably in *Pheidole*, *Monomorium*, *Meranoplus*, *Prolasius* and *Melophorus*, depend on seed harvesting for much of their food, and may accumulate large seed stores in the nests. Aspects of this behaviour are reviewed on pp. 70–1. Ants of these and many other non-harvesting genera are often involved in myrmecochory (see pp. 82–3 and below), and probably obtain significant nourishment from the elaiosomes of appropriate seeds. Prey and other food material returned to nests is placed with the larvae, which feed avidly upon it. Liquid food is passed between workers, and to queens and larvae, by regurgitative trophallaxis, and in many ants the queen and larvae receive worker-laid, 'trophic' eggs.

The major, general tasks of worker ants, including care



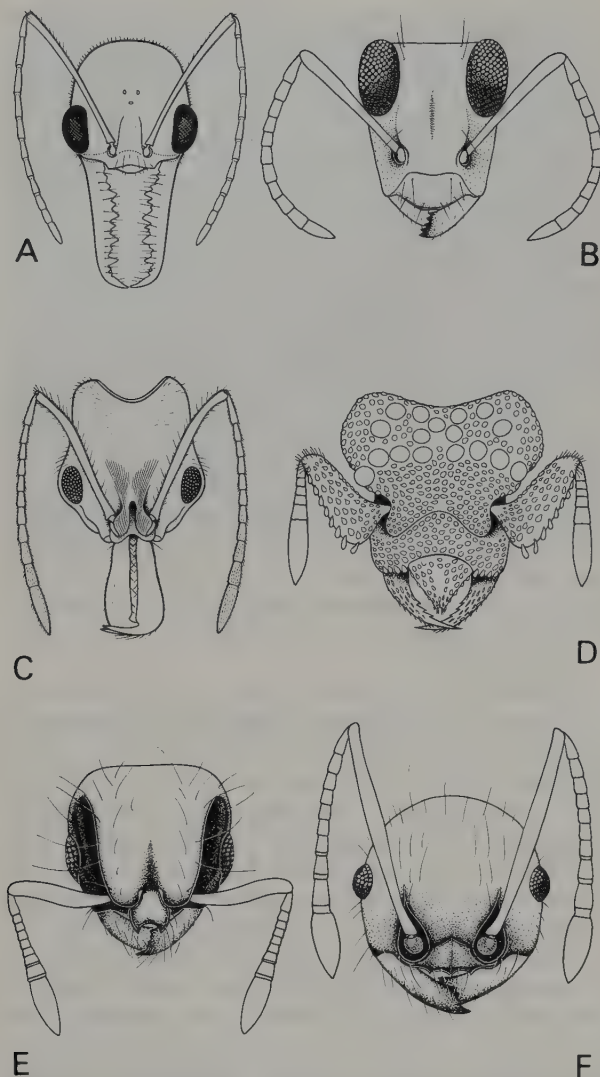


Fig. 42.39 Heads, frontal, of ants: A, *Myrmecia nigriceps*, Myrmeciinae; B, *Opisthopsis haddoni*, Formicinae; C, *Anochetus* sp., Ponerinae; D, *Rhopalothrix orbis*, Myrmicinae; E, *Mayriella abstinens*, Myrmicinae; F, *Pristomyrmex wilsoni*, Myrmicinae. [F. Nanninga]

of the queen and brood, nest maintenance and sanitation, and foraging, are seldom all performed by each worker in a nest at the same time. Age-based 'polyethism', or division of labour, is known in several groups, where workers shift to new tasks as they age, in approximately the sequence given above. Worker polymorphism is related to caste-based polyethism, in which majors are specifically adapted for nest defense, and are aptly called 'soldiers'. The very large, extremely large-headed, majors in some harvesting ants are specialist seed-crackers, and the 'bouncers' of the dacetine *Orectognathus versicolor* have toothless, rod-like mandibles with a labral jaw-trap mechanism. The jaws are snapped against alien ants invading the nests, causing their ballistic eviction. Worker behavioural pluripotency, possibly without polyethism, is evidenced in some *Amblyopone* species, and in *Nothomyrmecia*.

Communication between individuals is important in

social animals. The known media in ants are (1) olfactory e.g. alarm or trail-marking pheromones; (2) gustatory, particularly during food exchange by regurgitation; (3) auditory, including tapping, stridulation or other sounds transmitted mainly through the substrate; (4) mechanical, including antennal contact, body recoil, etc.; and (5) visual in those forms with well-developed eyes.

Two main kinds of orientation are involved in foraging by ants. Primitive species navigate visually (as was likely in their non-eusocial ancestors), and individual foragers learn restricted areas in which they hunt repeatedly. In some nocturnal species the image of the tree canopy silhouetted against the sky above is used as a navigational map. More advanced species use chemical trails involving pheromones produced by assorted gastral glands, which vary between taxa. These glands are usually associated with the sting or hind gut, or even with the legs (*Crematogaster*). Foraging activity by workers is often induced by contact with trail pheromones deposited by food-laden nest mates returning to the nest. In some species tandem- or chain-running by workers maintaining antennal contact, following a leader, is used to mobilise foragers to rich sources of food. Pheromones produced by hungry larvae probably induce foraging in many species, and well-provisioned colonies may temporarily cease foraging, perhaps in the absence of such pheromones. Trail pheromones are used to orientate migratory trails when colonies move to new nest sites, and tandem running or physical transport of some workers by others is not uncommon on such occasions. The latter seems to be involved in the 'teaching' of foraging zones to newly emerged workers of some *Rhytidoponera* species. Foraging activity may be precisely timed. Some species are strictly nocturnal (e.g. *Nothomyrmecia*, *Notostigma*, many dacetines, *Camponotus*, some *Polyrhachis*), while others may restrict diurnal foraging to the hottest times of day (*Melophorus*, some *Monomorium* and *Iridomyrmex*). Foraging may be curtailed when microclimatic conditions are unsuitable, and exodus from nests may be spectacular when diurnal conditions reach appropriate levels (*Iridomyrmex purpureus* with rising morning temperatures, *Nothomyrmecia* at nightfall). Nocturnality of foraging is far more prominent in formicids than in any flying, nest-building Hymenoptera (where it is very rare), and this is perhaps related to the relative ease of visual or chemical navigation by pedestrian ants.

Many predators commonly thought to eat ants, such as the numbat (*Myrmecobius fasciatus*) and the echidna (*Tachyglossus aculeatus*), actually feed primarily on termites and less often on ants. A number of Australian birds are frequent ant feeders, including the magpies (*Gymnorhina*), the coachwhip bird (*Psophodes*), and the thickhead (*Pachycephala*). Various agamid lizards feed extensively on ants in arid areas; of these *Moloch horridus* is a specialist predator of small *Iridomyrmex* species. Frogs (e.g. *Pseudophryne corroborae*) and spiders take many ants in Australia, as possibly also do the burrowing typhlopoid snakes. Antlions (Neuroptera) exact their toll on ants. Many arthropods live asinquilines in ant nests and feed on ant larvae or adults, or on secretions, the



food stores, or cast-off wastes of ants. Inquilines include some Collembola, Thysanura, Hemiptera, Neuroptera, Coleoptera (see pp. 560–1), Lepidoptera (Lycaenidae), Diptera (Phoridae, Syrphidae, Milichiidae), Hymenoptera (Diapriidae, Bethyidae) and various mites.

Ants are hosts to various parasites, including ascomycete fungi (*Cordyceps* and *Laboulbenia*), gregarines, juvenile mermithid nematodes and the metacercarial stages of certain platyhelminths. Internal and external parasitic insects include certain phorid flies, Strepsiptera and Eucharitidae, among others.

Ant colonies may contain as few as ten adults, or up to millions, but colony size in most Australian species is under 2000 workers. Colonies may, however, be extremely numerous in tropical forest, savannah woodland, or semi-desert, like that covering so much of Australia. It is not uncommon to find 20 or 30 nests of different species in a single large rotting log, or even two or three colonies under the same stone. Upwards of 120 species have been found in a few hectares of lowland rainforest in far North Qld and similar counts have been accumulated in areas of a few hectares in more southern *Eucalyptus* woodlands and mallee, even in arid areas. Sympatric assemblages may include many congeneric species (notably in *Myrmecia*, *Rhytidoponera*, *Monomorium*, *Meranoplus*, *Pheidole*, *Melophorus*, *Stigmacros* and *Iridomyrmex*).

Their ubiquity, abundance and high rates of activity qualify the Formicidae as one of the most ecologically important and generally prominent animal groups in all Australian terrestrial environmental systems. Ants tend to be active through the seasons. As predators and scavengers of other arthropods their operations are probably broadly beneficial, and the distributions of many other kinds of insects, including especially sawflies, predatory beetles and termites are strongly influenced by the presence or absence of ants in their niches. The transport of soil particles by ants upward from lower horizons is important in the aeration, vertical mixing and formation of soils.

Harvesting ants may cause damage by attacking crop seed-beds or collecting the seeds of forest trees, but the main agricultural impact of ants relates to their maintenance of aphids and coccids harmful to crops, often as vectors of plant diseases; some hemipterans are a serious threat only when attended by ants. 'Tramp' or 'vagrant' ant species such as the Argentine ant (*Iridomyrmex humilis*), black house ants (*Technomyrmex albipes* and *Iridomyrmex glaber*) and the hospital ant (*Monomorium pharaonis*) are pests in houses in the southern regions, while the Madeira ant (*Pheidole megacephala*), a fire ant (*Solenopsis geminata*), the ghost ant (*Tapi-noma melanocephalum*) and the assertive *Monomorium destructor* are familiar nuisances in tropical areas. Bush pests include the ferociously stinging bulldog and jumper ants of the genus *Myrmecia* (several of which are notoriously able to induce severe allergic reactions in stung humans), the mainly nocturnal sugar ants (*Camponotus* spp.), and the meat ants (*Iridomyrmex purpureus* group), which may also invade stores and dwellings.

Ants are rarely involved in the pollination of flowers.

This is believed to be because antibiotic chemicals produced by the metapleural glands, presumably for nest hygiene, are also lethal to pollen which has come in contact with ants. Some floral structures are now believed to be adaptations for the exclusion of ants. Some *Myrmecia* males lack metapleural glands, and, interestingly, those of at least one species engage in pseudocopulatory pollination of orchids.

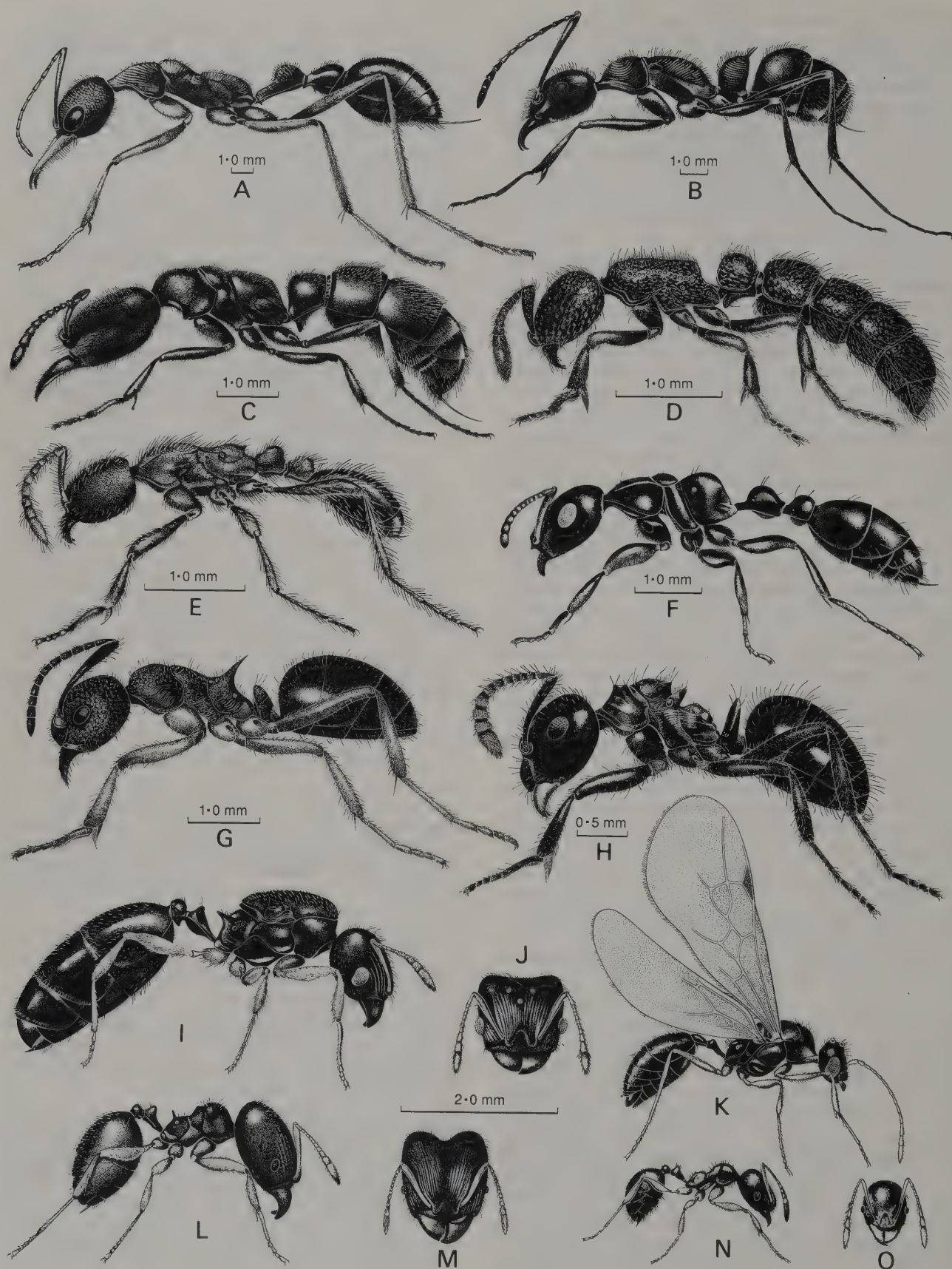
Many Australian ants participate in the symbiotic relationship of myrmecochory with certain plant species. Special structures (elaiosomes), which grow attached to seeds (Fig. 3.15), are attractive to ants. Workers gather such seeds, feed their larvae with elaiosome material, and redistribute the still viable seeds. This apparently aids significantly in dispersal and protection of seeds from harvesting or predatory animals, and perhaps from fire. The species richness and taxonomic diversity of both the ants and plants involved in myrmecochory demonstrates its likely importance in Australian semi-arid and sub-humid woodlands and forests (see also pp. 82–3).

Nine subfamilies of ants occur in Australia; those not represented are the Neotropical Ecitoninae, and the Sri Lankan Aneuretinae. *Nothomyrmecia macrops* (NOTHOMYRMECINAE) is generally considered to be the most primitive living formicid. Subfamily MYRMECINAE (only *Myrmecia*) is very primitive, and is restricted almost exclusively to Australia, with a single species on New Caledonia. This subfamily is represented elsewhere by the extinct Oligocene genera *Prionomyrmex* (from Baltic amber), and *Ameghinoa* (Argentina). *Myrmecia* and *Nothomyrmecia* together cover the whole range of chromosome numbers known for the Hymenoptera, and are exceptionally diverse in this regard. An undescribed *Myrmecia* of the *pilosula* group is one of only two eukaryote animals known to have only a single pair of chromosomes; *Nothomyrmecia* has 47 pairs. Among the other subfamilies PONERINAE (including Cerapachyini) are exceptionally rich in species, while DORYLINAE and PSEUDOMYRMECINAE are represented only by a few Indo-Malayan elements, largely restricted to the north. Records of males show LEPTANILLINAE to be very widespread, but few workers are known.

#### Key to the Subfamilies of Formicidae Known in Australia—Workers

(Where there are two figures in the square brackets, the first is the number of genera and the second the estimated number of *validly named* species and subspecies known from Australia. Those genera marked \* were illustrated in Fig. 37.40 of the 1st edition.)

1. Pygidium (dorsal part of terminal exposed gastral tergum) flattened at apex, flattened part bordered with denticles arranged in rows on each side; underside of head with strong carina on each side running forward from posterior corner [Cerapachyini—*Cerapachys* (\* as *Lioponera*), *Sphinctomyrmex* (Fig. 42.40D); 2 genera, 60 spp.] ..... PONERINAE (pt)
- Pygidium simple; underside of head without distinct carinae extending forward from posterior corners ..... 2





- 2(1). Gaster attached to mesosoma by waist consisting of 2 more or less reduced and nodiform segments (Figs 42.34, 40A, E, F, L) ..... 3  
 Gaster attached to mesosoma by waist consisting of single segment, which may be nodiform, erect or inclined and scale-like, or even prostrate and more or less hidden by overhanging gaster (Figs 42.36, 40B, C, G, H) ..... 7
- 3(2). Larger species, length usually exceeding 8 mm; eyes large; mandibles long, slender, serially dentate ('bulldog ants') [*Myrmecia* (Figs 42.39A, 40A); 90 spp.] ..... MYRMECINAE  
 Smaller species, or, if largest workers or soldiers are over 8 mm, eyes very small or absent and/or mandibles not elongate ..... 4
- 4(3). Eyes absent; small to minute army ants [queens dichthadiiform, i.e. blind, wingless, with simple mesosoma, gaster long and bulky] ..... 5  
 Eyes large to minute, but normally clearly represented in Australian species; not army ants ..... 6
- 5(4). Extremely minute (less than 2.5 mm), slender, yellow species, with 12-segmented antennae. [Rare but widespread, and subterranean; *Leptanilla*; 1 sp.] ..... LEPTANILLINAE  
 Small species, but usually more than 2.5 mm long; antennae 10-segmented [*Aenictus* (Fig. 42.40E); 4 spp.] ..... DORYLINAE
- 6(4). Tarsal claws toothed; tibial spurs of mid and hind legs distinctly pectinate; Australian species very slender, black, with large eyes; inhabiting hollow twigs and similar plant cavities [*Tetraponera* (Fig. 42.40F); 3 spp.] ..... PSEUDOMYRMECINAE  
 Tarsal claws simple; tibial spurs of mid and hind legs, when present, simple or at most very indistinctly pectinate; body form and nesting habits very diverse [e.g. *Podomyrma*, *Tetramorium* (Fig. 42.34), *Pheidole* (Fig. 42.40I–O), *Meranoplus*, *Strumigenys*, *Rhopalothrix*, *Mayriella* (Fig. 42.39E); 34 genera, 340 spp.] ..... MYRMICINAE
- 7(2). Sting well developed and functional, usually extended and visible in dead specimens ..... 8  
 Sting absent, or vestigial and not extensible ..... 9
- 8(7). Large (ca 10 mm), tawny yellow species with large convex eyes set at the middle of the sides of the head; mesosoma and petiole much as in *Myrmecia*; 2nd gastral segment non-tubulate; tarsal claws toothed [Eyre Peninsula, S.A., and presumably south-western W.A.; *Nothomyrmecia* (Fig. 42.36); 1 sp.] ..... NOTHOMYRMECINAE  
 Disagreeing with some or all of the above characters; 2nd gastral segment tubulate, with collar inserted into preceding segment, 1st gastral segment posteriorly sometimes constricted [e.g. *Amblyopone* (Fig. 42.40C), *Rhytidoponera*,\* *Diacamma* (Fig. 42.40B), *Leptogenys*, *Anochetus* (Fig. 42.39C); 22 genera, 200 spp.] ..... PONERINAE (pt)
- 9(7). Terminal gastral sternum rolled into short, ventro-apical cone with round, apical orifice (with or without

coronula of minute hairs) serving as nozzle for defensive acid spray; metapleural gland present or absent [e.g. *Melophorus*, *Prolasius*,\* *Notoncus* (Fig. 42.40H), *Acropyga*, *Oecophylla* (Fig. 42.47), *Camponotus*, *Polyrhachis*, *Opisthopsis* (Fig. 42.39B); 20 genera, 420 spp.] ..... FORMICINAE  
 Gastral apex without such an acid-spray ejecting cone; defensive secretion a viscous fluid ejected through a slit-like orifice on face of terminal sternum, metapleural glands present [e.g. *Leptomyrmex*, *Dolichoderus* (Fig. 42.40G), *Iridomyrmex*,\* *Technomyrmex*; 10 genera, 150 spp.] ..... DOLICHODERINAE

The described Australian ants were catalogued by R. W. Taylor and D. R. Brown (1985). A bibliography of taxonomic papers is included in the Australian regional checklist of R. W. Taylor (1987). P. J. M. Greenslade (1979) characterises and keys the ant genera of S.A., and reviews their bionomics.

Information on larvae of many Australian ants was summarised by Wheeler and Wheeler (1976). Matters of significance in adult morphology and physiology are reviewed by Gotwald (1969—mouth-parts); W. L. Brown and Nutting (1950—wing venation), R. W. Taylor (1978—abdominal exoskeleton), Eisner (1957—proventriculus), Kugler (1978—sting morphology), Piek (1986—venom chemistry). Chromosomal morphology and its evolution in Australian ants are reviewed by Imai *et al.* (1977). Important source texts or reviews on ant biology are those of E. O. Wilson (1971, 1975), Sudd and Franks (1987), Beattie (1985), Oster and Wilson (1978), papers in Hermann (1979–82), and Hölldobler and Wilson (1990), which illustrates and keys (regionally) world genera.

### Superfamily SPHECOIDEA

Predatory or cleptoparasitic. Predominantly solitary; some species nesting communally, with varying degrees of social behaviour. Pronotum more or less freely articulating with mesothorax; posterolateral angle dorsal to spiracle cover lobe not reaching tegula; cover lobe sometimes reaching tegula; ventral angles of pronotum produced, almost meeting mid-ventrally; prepectus fused to mesepisternum. Metapostnotum greatly enlarged and posteriorly produced to form dorsum of apparent propodeum. Hind basitarsus not markedly wider than following segments, with calcar in slight depression. T8 of female mid-dorsally narrowly sclerotised. Larvae variable, sometimes with paired spinnerets; maxilla usually with 2 papillae (palp and galea). Cocoon present.

The Sphecoidea and Apoidea are closely related and some authors combine them in a single superfamily.

**64. Sphecidae** (Plates 5, Q, 6, P, R, X; Figs 42.41, 42). Small to large size (1.5–39 mm). Antennae generally 12-segmented in female, 13-segmented in male. Differ from Apoidea in lacking branched hairs and broad, flattened

hind basitarsus. Females of fossorial forms often with specialised structures for digging, e.g. rakes of modified tarsal setae; expanded or spinose legs; or last visible metasomal tergum with a more or less flattened, soil-pushing, pygidial plate defined by carinae. Ampulicinae retain many plesiomorphic morphological and behavioural features and are possibly the sister group of all other subfamilies. Probably Sphecinae and Pemphredoninae also diverged relatively early. The Crabroninae is either the sister group or a subgroup of the Larrinae (Lomholdt 1985). The small subfamilies Heterogyninae, Astatinae, Laphyragoginae, Entomosericinae and Xenosphecinae are extralimital.

Adults feed on nectar or honeydew, or at extrafloral nectaries and females (except those of cleptoparasitic species) hunt spiders or various hexapods for larval food. In the most behaviourally primitive species, the host is located and stung in its own burrow; the female sphecid constructs no nest and the life cycle is thus similar to that in many parasitic Hymenoptera. In behaviourally more advanced species, the prey is dragged or carried in flight to a pre-existing niche or a specially excavated or constructed nest. *Larra* drags its relatively large prey gripped in its mandibles. Other sphecids fly to their nests with prey grasped by the mandibles (e.g. some Pemphredoninae and Sphecinae), legs (e.g. most Nyssoninae) or special carrying devices (e.g. some Philanthinae), or impaled on the sting (some Crabroninae). More sophisticated and efficient prey carriage allows speedier provisioning of the nest, and, often, exploitation of smaller prey. Ampulicinae are unusual in that they lead their lightly paralysed, still ambulatory cockroach prey to their nest. Oviposition may precede or follow provisioning. In some species the wasp larva hatches soon after the first prey has been added to the cell and the larva is then fed progressively, with the female sealing the larval cell only as the larva ceases to feed. Communal nesting has been recorded in Sphecinae, Pemphredoninae, Crabroninae, Larrinae, Nyssoninae and Philanthinae, and in some *Cerceris* (Philanthinae) and some Pemphredoninae co-operation and division of labour among communal conspecifics identify advanced, social (and sometimes eusocial) behaviour.

Some species of Sphecidae are highly specialised predators, hunting only one or two closely-related prey species. Others are more generalised and exploit local abundances of a variety of prey.

#### Key to the Subfamilies of Sphecidae Known in Australia

1. Metasoma with cylindrical petiole formed by 1st apparent metasomal sternum (S2) only (Figs 42.10D, 41D, K); hind wing with large jugal lobe (anal and jugal notches more or less coincident) and anal vein posterior to 1A ..... SPHECINAE
- Metasoma variable, if with cylindrical petiole formed by S2 only, then hind wing with very small jugal lobe and without anal vein posterior to 1A ..... 2
- 2(1). Notauli deep, occupying entire length of mesoscutum; mid tibia with 2 spurs; tarsal claws each bifid; jugal lobe of hind wing small or absent (Fig. 42.41j) ..... AMPULICINAE

- Without above combination of character states ..... 3
- 3(2). Mid tibia with 1 spur; petiole formed by S2 only (Fig. 42.41o) ..... PEMPHREDONINAE
- Without above combination of character states ..... 4
- 4(3). Pre-pterostigmal length of 1st submarginal cell in fore wing much more than half total cell length (Figs 42.41i, M) ..... NYSSONINAE-Stizini, Bembicini
- Pre-pterostigmal length of 1st submarginal cell in fore wing at most about half total cell length (Figs 42.41A, C, E-H, L) ..... 5
- 5(4). Mid tibia with 2 apical spurs ..... NYSSONINAE-Nyssonini, Gorytini (pt)
- Mid tibia with 1 apical spur ..... 6
- 6(5). Hind ocelli deformed or represented by scars (Figs 42.42A, C) ..... LARRINAE-Larrini
- Hind ocelli normal ..... 7
- 7(6). Inner orbits notched or angulate (Fig. 42.41L) ..... LARRINAE-Trypoxylini
- Inner orbits entire ..... 8
- 8(7). Metasoma with node-like 1st segment and constrictions between segments (Fig. 42.41B, C) ..... PHILANTHINAE
- Metasoma not as above ..... 9
- 9(8). Fore wing with 1 submarginal cell (Fig. 42.41A) ... 10
- Fore wing with 2 or 3 submarginal cells (Figs 42.41E-H) ..... 11
- 10(9). Scape about as long as basal 3 flagellar segments combined ..... CRABRONINAE
- Scape much shorter than basal 3 flagellar segments combined ..... LARRINAE-Miscophini (pt)
- 11(9). Mandible externally notched ..... LARRINAE-Miscophini (pt)
- Mandible not externally notched ..... NYSSONINAE (pt)

AMPULICINAE (12 spp.; 4–14 mm). Females paralyse cockroaches which they lead to a concealed place for oviposition. Their predatory behaviour is primitive in that there is only one cockroach per nest and that the nest site is located after prey-capture. Fore wings banded, especially in females, in the endemic genera *Aphelotoma* (8 spp.; Fig. 42.41j) and *Austrotoma* (1 sp.). *Aphelotoma* are attracted to sunlit, smooth-trunked *Eucalyptus* trees where their jerky movements mimic those of ants. Females forage in litter around the base of trees. *Dolichurus* (3 spp.), in which the antennal bases are covered by a median lobe, is well represented outside Australia; adults fly rapidly, alighting momentarily on sunny leaves in forests.

SPHECINAE (48 spp.), in which S2 forms a cylindrical petiole, includes many large and familiar 'mud-daubers' and 'digger wasps'. Some extralimital species maintain several nests simultaneously or show primitive social behaviour.

Sceliphriini: *Sceliphron* (3 spp.; 18–39 mm) are black with yellow markings and provision with spiders. Nests of *Sceliphron laetum* (Plate 6, R; Fig. 42.41D), the common mud-dauber, are often large and multi-tiered; cells are covered with extra, rough-surfaced layers of mud. *Sceliphron formosum* builds simple clusters of cells. *Sceliphron caementarium*, accidentally introduced from the New World, has become established in south-eastern Qld. The metallic blue *Chalybion bengalense* (15 mm) nests in pre-existing cavities in northern Australia.



Ammophilini (14–33 mm) are fossorial predators on lepidopterous larvae. In *Ammophila* (10 spp.) the metasomal stalk (T2 + S2) is longer than the rest of the metasoma, and S2 and S3 are widely separated. In the one central Australian species of *Parapsammophila* the tarsal claw has basal teeth. *Podalonia tydei*, in which the tarsal claw is simple, is widespread through the southern Palaearctic and Oriental regions, Australia and New Zealand; common in sandy areas, females capture prey before digging a nest. Stones held in the mandibles are used by some *Podalonia* and *Ammophila* as tools to compact material in burrows.

Sphecini (8–34 mm) are robust, generally dark-coloured predators on Orthoptera. *Sphecx* (24 spp.; Fig. 42.41k) is fossorial and provisions with Gryllidae and Tettigoniidae; some species have attractive golden markings or pubescence. *Prionyx* (2 spp.) is fossorial and preys on Acrididae; adults of both sexes are territorial. *Isodontia* (6 spp.) nests in pre-existing cavities, especially in wood, and uses grass stems and seeds to construct cells and close the nest entrance; females prey on Gryllidae and Tettigoniidae.

PEMPHREDONINAE (92 spp.). Generally overlooked because of their small size (1.5–9 mm) but often abundant; mostly predatory on Hemiptera and Thysanoptera, with some extralimital species hunting Collembola. Head rather cuboidal, fore wing pterostigma large, mid tibia with 1 spur; metasoma sessile in most Australian species, but if tubular petiole distinct this formed by S2 alone. Some extralimital genera have the most reduced wing venation in the Sphecidae. *Psenulus* (2 spp.), with 3 fore wing submarginal cells, occurs in North Qld and the Oriental region. All other Australian genera have 2 fore wing submarginal cells. The head is massive and the face concave in the endemic *Paracrabro* (1 sp.; Figs 42.41N, O) from the south-east. *Polemistus* (2 spp.), with a tubular petiole and closed 2nd discoidal cell in the fore wing, also occurs in the Oriental region. *Arpactophilus* (50 spp.), with occipital and adorbital carinae, a sessile metasoma and often coarse sculpturing, has radiated in Australia, New Guinea and New Caledonia. One subsocial species constructs a silken nest in abandoned mud nests of other wasps. Species of *Spilomena* (35 spp.), a cosmopolitan genus, generally lack occipital and adorbital carinae, have a sessile metasoma and are more finely sculptured than *Arpactophilus*. *Spilomena* nests in pre-existing cavities in wood or walls or in the soil, and preys on Thysanoptera or small wasps.

LARRINAE (267 spp.; 5–23 mm). In Larrini the lateral ocelli are modified, sometimes with near-complete loss of the lens (Fig. 42.42). Australian species belong to large, widespread genera and prey on Orthoptera. Females of *Larra* (3 spp.) construct no nest; they temporarily paralyse Gryllotalpidae and lay one egg per host. The wasp larva eventually kills the host and pupates in the host burrow. *Liris* (15 spp.) nests in pre-existing, subterranean burrows provisioned with Gryllidae. *Tachytes* (12 spp.) is fossorial; extralimital records indicate various families of Orthoptera as prey. *Tachysphex* (40 spp.) is fossorial and preys on Acrididae, Mantodea and Blattellidae (BLAT).

The ocelli are normal and the inner orbits straight or slightly sinuate in Miscophini. *Sericophorus* (74 spp.; Fig. 42.41G), fossorial and predatory on adult muscoid flies, has 12-segmented antennae in both sexes, and is restricted to Australia and New Guinea. *Sphodrotes* (12 spp.) and *Auchenophorus* (3 rather ampulicene-like species with banded wings) are both endemic. *Lyroda* (11 spp.) and *Nitela* (3 spp.) are widespread outside Australia.

Ocelli are normal and the orbits distinctly emarginate in Trypoxylini. Both Australian genera prey on spiders. The metasoma is long and slender and there is one fore wing submarginal cell in *Trypoxylon* (Fig. 42.41L). Each of the 7 Australian species also occurs in the New Guinea-Oriental region. The metasoma is more compact and the fore wing has 2 or 3 submarginal cells in *Pison* (80 spp.), a cosmopolitan genus best represented in Australia and South America. Australian species of *Pison* nest in pre-existing cavities, construct free mud-nests or are fossorial. Several species have spread to various Pacific islands and New Zealand.

CRABRONINAE (79 spp.; 3.5–18 mm). Head cuboidal, inner orbits not strongly emarginate, ventrally converging; fore wing with one submarginal cell. Hind wing jugal lobe small. Primitively fossorial, secondarily nesting in pre-existing cavities and twigs. Mostly predatory on Diptera although a few extralimital genera provision nests with various orders. In most Australian genera the metasoma is pedunculate and slender. *Rhopalum* (30 spp.) is a cosmopolitan genus including both fossorial and twig nesting species. Ground nesting *Podagrirus* (20 spp.) occurs in South America, Australia and New Zealand. Species of the endemic *Pseudoturneria* (3 spp.) lack a median notch on the pronotum. T2 is spinose in the endemic *Notocrabro* (2 spp.). Of the genera in which the metasoma is more sessile and robust and the pronotum has a distinct median notch, *Williamsita* (9 spp.; Plate 6, P; Fig. 42.41A), nesting in rotting logs and preying on Calliphoridae, is restricted to Australia, New Caledonia and Vanuatu, *Chimiloides* (3 spp.) is endemic, and *Ectemnius* (4 spp.) and *Lestica* (1 sp.) are better represented outside Australia.

NYSSONINAE (146 spp.). Fore wing with 3 submarginal cells in all Australian Nyssoninae except *Acanthostethus* which has 2. First submarginal cell long prestigmally and scutellum posteriorly overlapping metanotum in the closely-related Stizini and Bembicini. Fossorial.

Nyssonini: *Acanthostethus* (15 spp.; 5–9 mm) is endemic; species are heavily sclerotised with posterolateral propodeal spines (Fig. 42.41H) as in Chrysidinae, and cleptoparasitic on *Sericophorus*. Gorytini are mostly medium sized (7–17 mm) and all prey on auchenorrhynchous Hemiptera. *Sphecius* (1 sp.; Fig. 42.41E) and the endemic *Exeirus* (1 sp.; Plate 5, Q; Fig. 42.41F) are the large (20–35 mm) 'cicada killers'. *Austrogorytes* (23 spp.) is endemic, *Argogorytes* (4 spp.) and *Ammatomus* (3 spp.) are well represented elsewhere and *Clitemnestra* (10 spp.; Plate 6, X) is known only from Australia and South America. *Clitemnestra*, *Argogorytes* and *Exeirus* are amongst the least specialised gorytines.

Stizini: *Bembecinus* (14 spp.; 5–11 mm; Fig. 42.41M)

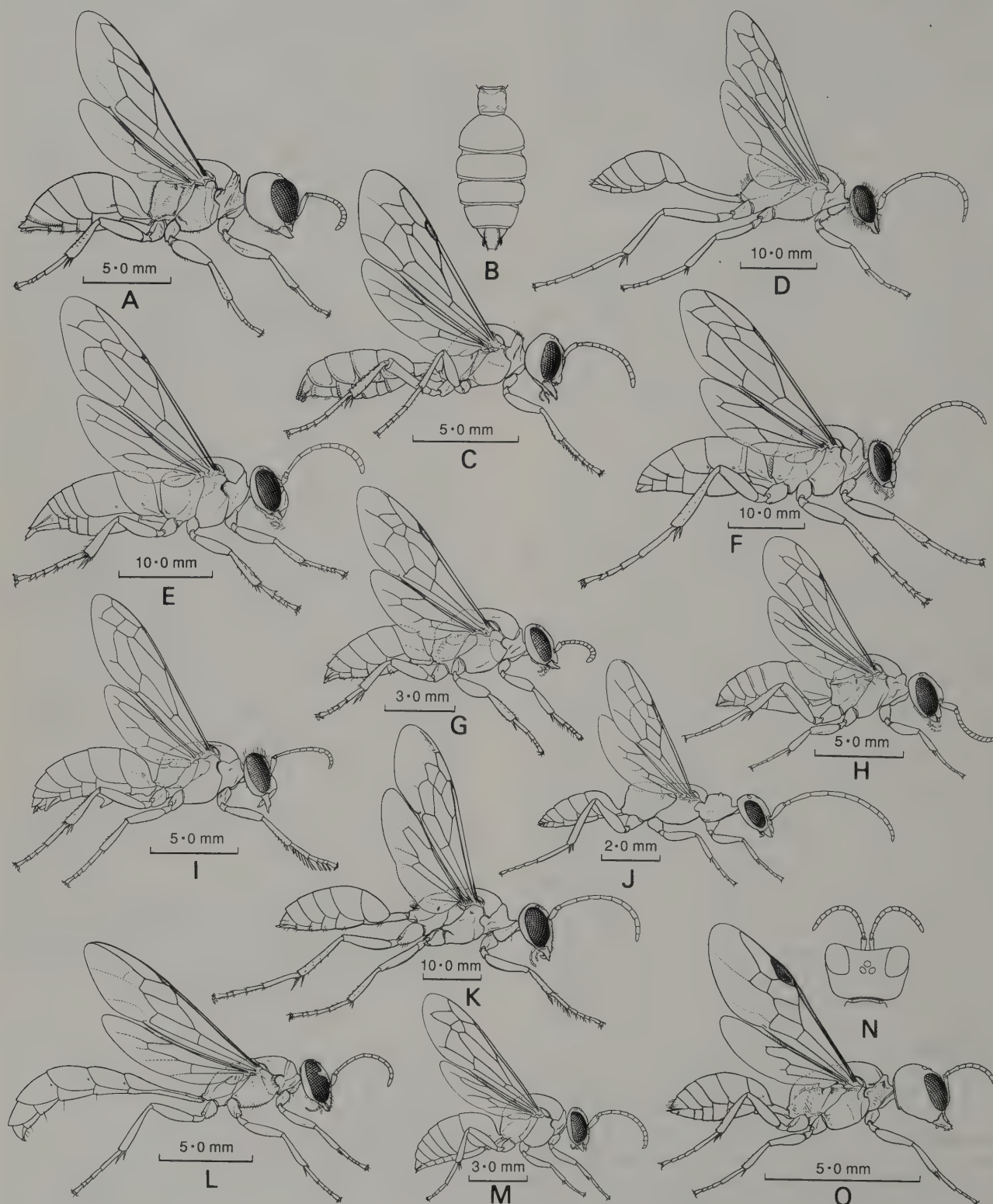


Fig. 42.41 Sphecidae: A, *Williamsita* sp., Crabroninae; B, *Cerceris* sp., Philanthinae, metasoma, dorsal; C, same; D, *Sceliphron laetum*, Sphecinae; E, *Sphecius pectoralis*, Nyssoninae; F, *Exeirus lateritius*, Nyssoninae; G, *Sericophorus* sp., Larrinae; H, *Acanthostethus* sp., Nyssoninae; I, *Bembix* sp., Nyssoninae; J, *Aphelotoma* sp., Ampulicinae; K, *Sphegus* sp., Sphecinae; L, *Trypoxylon* sp., Larrinae; M, *Bembecinus* sp., Nyssoninae; N, *Paracrabro froggati*, Pemphredoninae, head, dorsal; O, same.

[M. Quick]



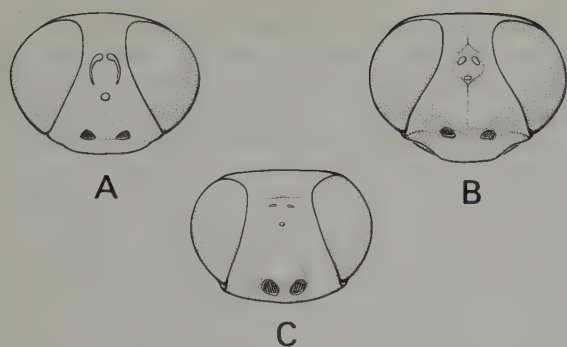


Fig. 42.42 Sphecidae-Larrinae, ocellar region: A, *Tachytes* sp.; B, *Tachysphex* sp.; C, *Larra* sp. [S. Monteith]

is a large, cosmopolitan genus. Females progressively provision with auchenorrhynchous Hemiptera and close their nest before each flight. Some species are sexually dichromatic, with xanthic males. Bembicini: *Bembix* (83 spp.; 7.5–25 mm) with reduced ocelli and a large, exposed labrum (Fig. 42.41i), is a large, cosmopolitan genus most diverse in Australia and Africa. Species are commonly black with extensive yellow markings and fly rapidly. Australian species provision their nests with flies or (less often) bees, other wasps, adult Myrmeleontidae (NEUR) or Zygoptera (ODON).

PHILANTHINAE. In the cosmopolitan genus *Cerceris* (100 spp.; 5–25 mm) the 1st metasomal segment forms a petiole, the metasoma is constricted between segments, the head is wide, and the hind femur apically expanded and flattened (Figs 42.41b, c). Species nest in bare, firm ground, often in aggregations, and prey on small, adult Coleoptera. Nests are left open between flights. Several Australia species nest communally and there is some division of labour. [Bohart and Menke 1976; Cardale 1985; Lomholdt 1985]

### Superfamily APOIDEA

by C. D. MICHENER and T. F. HOUSTON

Adults usually provision larval cells with pollen and nectar or (rarely) floral oils; a few species cleptoparasitic. Predominantly solitary; some species nesting communally, some social. Pronotum, metapostnotum, metapleuron as in Sphecoidea. In many groups hind basitarsus of female wider than following tarsal segments. T8 completely divided to form hemitergites. At least a few branched hairs present. Larvae variable; maxilla usually with only 1 papilla (palp), galea absent.

It is generally accepted that the bees arose from a sphecoid ancestor (Brothers 1975; Bohart and Menke 1976; Lomholdt 1982) although Lanham (1981) argued that the similarities between bees and sphecoids could be the result of convergence. Lanham suggested that the bees are more closely related to some vespoid families.

Because of their short, obtuse or bifid glossa, which superficially resembles that of sphecoids, the colletes have long been considered to be the most primitive of the living bees. However, recent detailed comparisons of the glossae of bees and wasps indicate that the truncate or bifid condition in colletes is derived and the short acute

condition (as found in andrenids and halictids) is ancestral (McGinley 1980; Michener and Brooks 1984).

Bees are basically sphecoid wasps that use pollen rather than insect or spider prey as a protein source for their larvae. There are some 20 000 species world-wide, ranging from forms only 2 mm long to giants attaining 39 mm, and in Australia there are many undescribed species.

The great majority of bees are solitary, each female performing all tasks necessary for the production of offspring. The nest typically consists of a burrow in the soil, in wood, or in a pithy stem, from which lateral burrows extend to the cells, or which is itself subdivided into cells. Some solitary bees, however, construct cells of resin, mud or other materials in protected or exposed situations. Normally each cell is completed, provisioned with pollen and honey, an egg laid in it, and sealed, before the next cell is begun; but in many Halictidae this sequence is broken, and new cells are started before their predecessors are completed. The mother ordinarily dies before her progeny reach maturity and emerge from their cells. Many bees provide for their young in this way and are called solitary even though they nest gregariously. Sometimes aggregations may consist of thousands of nest burrows, each made by a single female, in a few square metres of soil. Some bees (e.g. many Halictidae) are communal—two or more females share a nest entrance but construct their own burrows and cells. Still others live in small, more or less social groups consisting of two to several females in a single nest. Finally, a few bees live in very large colonies with clearly differentiated female castes of worker and queen. The nesting behaviour of Australian bees has been studied by Hacker, Rayment, Michener and a few others (references in Michener 1965b), and more recently by Houston (1969–84b), Houston and Thorp (1984) and Knerer and Schwarz (1976, 1978), but it has not yet received due attention.

Cleptoparasitic or 'cuckoo' bees do not make their own nests. Adults oviposit in the cells of other bees and their larvae feed on provisions provided by the host, which is always some other species of bee. Cuckoo bees are scarcer in Australia than in any other region, perhaps because so many of the Australian bees are Colletidae, a family without or with very few cleptoparasitic species. The best known of the few Australian genera of cleptoparasites is *Thyreus* (Anthophoridae), species of which parasitise *Amegilla* (Anthophoridae). In *Thyreus*, *Nomada* (Anthophoridae) and *Coelioxys* (Megachilidae) the young larva has a large, heavily sclerotised head with huge, sharp mandibles for destroying the egg or young larva of the host. These structures have doubtless arisen independently in each of the three groups.

Bees are dependent on nectar from flowers as their chief source of carbohydrates and on pollen as their source of proteins. Many species obtain nectar from a wide variety of flowers, and some also gather pollen from many kinds of flowers. However, some restrict their pollen collecting to particular kinds of plants. Since most of the pollen that is gathered is used in provisioning cells for larvae, an activity in which only the females engage, it is primarily the females that show the restriction in

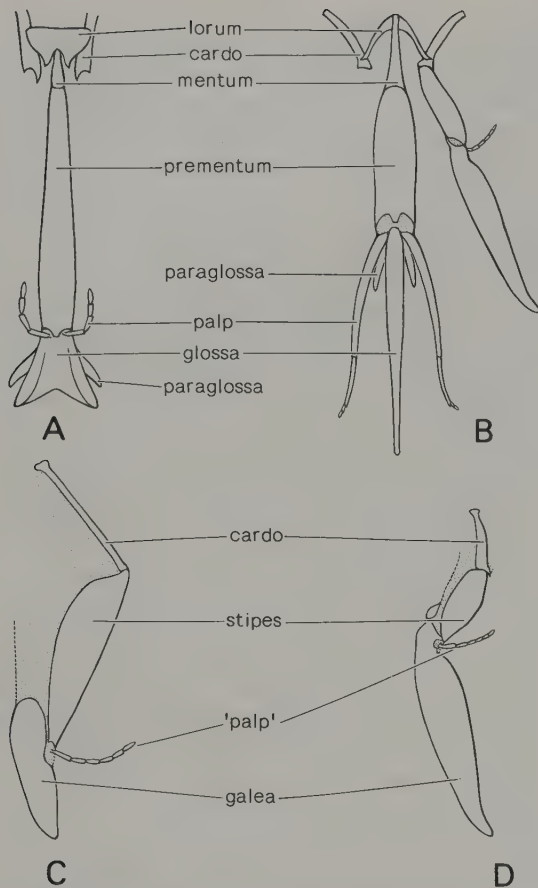


Fig. 42.43 Apoidea, mouth-parts: A, labium and maxillary cardines of a colletid; B, labium and maxilla of an anthophorid; C, maxilla of a colletid; D, maxilla of an anthophorid. [After Michener 1965b]

the kinds of plants they visit. Even in these species, the males and females gathering nectar may visit a variety of flowers. Bees that gather pollen from many kinds of

flowers are called *polylectic*, whereas those that gather from only a few species of related flowers are called *oligolectic*. Numerous hylaeine and euryglossine Colletidae carry pollen in the crop with the nectar instead of among scopal hairs on the legs and body. For such bees it is not easy to determine the degree of oligolecty, as very close observation is necessary to determine whether a female is gathering pollen or merely sucking nectar.

Australia is the only continent where most bees are largely dependent on a single family of plants, the Myrtaceae. Genera attractive to bees include *Angophora*, *Baeckea*, *Callistemon*, *Eucalyptus*, *Eugenia*, *Leptospermum*, *Melaleuca* and *Tristania*. Most bees oligolectic on Myrtaceae will collect pollen from whatever members of that family are in bloom in the area. Many polylectic forms also include Myrtaceae among their pollen sources. Some examples of other oligolectic relationships are: the subgenus *Cladocerapis* of *Leioproctus* (Colletidae) which forages only on *Persoonia* (Proteaceae); many species of *Trichocolletes* (Colletidae) which forage only on certain kinds of Fabaceae; and *Lithurge* (Megachilidae) which forages only on large-flowered Malvaceae, such as native species of *Hibiscus*. Many short-tongued bees of the family Colletidae are oligolectic on *Eremophila* (Myoporaceae) and some of them exhibit pronounced elongation of the palps and the proboscis as adaptations allowing them to collect nectar through a constriction in the tubular corolla (Houston 1983a).

Although very diversified in size, structure and appearance, the bees are not readily divisible into a few sharply defined major groups of equivalent status. For this reason their classification has never reached the stage of general agreement. Some workers would place them all in a single family, the Apidae, whereas others divide them into from two to many families. The classification adopted here (with some modifications) is that of Michener (1965b) who defined taxa down to subgenera, and provided an annotated list of Australian species and a bibliography.

#### Key to the Families of Apoidea Known in Australia

1. With 1 or 2 submarginal cells (Figs 42.45A–C, G, I) ..... 2
- With 3 submarginal cells (Figs 42.44A, 45D–F, H, J) ..... 8
- 2(1). Marginal cell open at apex (distal wing venation much reduced; Fig. 42.45B); hind tibia of worker with corbicula (smooth area surrounded by long hairs) on outer side ..... **Apidae** (pt, *Trigona*, p. 1000)
- Marginal cell closed at apex; corbicula absent ..... 3
- 3(2). Pterostigma almost absent and basal to middle of wing (very large bees) ..... **Anthophoridae** (pt, *Xylocopa*, p. 999)
- Pterostigma distinct, at or distal to middle of wing ..... 4
- 4(3). Inner hind tibial spur of ♀ greatly broadened basally so that whole spur is crescentic, concave margin with comb of numerous fine teeth (North Qld) ..... **Ctenoplectridae** (p. 998)
- Inner hind tibial spur not greatly broadened basally ..... 5
- 5(4). Arolia absent or essentially so ..... **Megachilidae** (pt, p. 999)
- Arolia present and conspicuous between claws ..... 6
- 6(5). Pterostigma very short, 0.3 times as long as costal margin of marginal cell or less (tropical) ..... **Megachilidae** (pt, *Anthidiellum*, p. 999)
- Pterostigma more than 0.5 times as long as costal margin of marginal cell ..... 7
- 7(6). Mesepisternum lacking pre-episternal groove (Fig. 42.5B) below scrobal suture; proboscis long, apices of galeae in repose reaching beyond posterior end of proboscidial fossa ..... **Anthophoridae-Allodapini** (p. 999)
- Mesepisternum with distinct pre-episternal groove below scrobal suture; proboscis shorter, apices of galeae in repose not reaching posterior end of proboscidial fossa ..... **Colletidae** (pt, p. 995)
- 8(1). Hind tibial spurs absent; hind tibia of worker with corbicula on outer side ..... **Apidae** (pt, *Apis*, p. 1000)



- Hind tibial spurs present; hind tibia without corbicula ..... 9
- 9(8). Marginal cell much shorter than 1st median cell; vein *cu-v* of hind wing strongly oblique (directed towards body posteriorly, Figs. 42.45H, J) and much more than 0.5 times as long as 2nd abscissa of M+CuA (except in *Nomada*) ..... **Anthophoridae** (pt, p. 999)
- Marginal cell little if any shorter than 1st median cell; vein *cu-v* of hind wing transverse and usually less than 0.5 times as long as 2nd abscissa of M+CuA (in *Stenotritidae* *cu-v* is elongate but directed away from body posteriorly) .... 10
- 10(9). Pterostigma almost absent (large robust bees) ..... **Anthophoridae-Xylocopini** (pt, p. 999)
- Pterostigma distinct, longer than broad ..... 11
- 11(10). Mesepisternum without pre-episternal groove; scopa of ♀ on tibia and basitarsus only; proboscis long, apices of galeae in repose reaching beyond posterior end of proboscival fossa ..... **Anthophoridae** (pt, *Ceratina*, p. 999)
- Mesepisternum with distinct pre-episternal groove which usually continues below scrobal suture; scopa of ♀ on femur and elsewhere (rarely absent); proboscis shorter, apices of galeae in repose not reaching posterior end of proboscival fossa ..... 12
- 12(11). 1st flagellar segment of antenna longer than scape (Fig. 42.44E) ..... **Stenotritidae** (p. 996)
- 1st flagellar segment shorter than scape ..... 13
- 13(12). 3rd submarginal cell at least 0.75 times as long as 1st and more than 2 times as long as 2nd (Fig. 42.45F); pre-episternal groove extending but little below scrobal suture ..... **Halictidae-NOMIINAE** (p. 998)
- 3rd submarginal cell usually less than 0.75 times as long as 1st and always less than 2 times as long as 2nd; pre-episternal groove extending well below scrobal suture (except in *Hesperocolletes*, Colletidae) ..... 14
- 14(13). Body with yellow integumental markings including abdominal fasciae (bees less than 6 mm long) ..... **Halictidae** (pt, *Nomioides*, p. 998)
- Body, especially abdomen, without yellow integumental markings or, at most, with a pale mark on clypeus of male ..... 15
- 15(14). 1st recurrent vein of fore wing interstitial with 2nd transverse cubital vein or almost so (Fig. 42.46A); 2nd recurrent and 3rd transverse cubital veins usually distinctly weaker than the aforementioned veins (except in *Sphecodes*) ..... **Halictidae-HALICTINAE** (except *Nomioides*, p. 998)
- 1st recurrent vein of fore wing entering 2nd submarginal cell about midway between 1st and 2nd transverse cubital veins (Fig. 42.44A); 2nd recurrent and 3rd transverse cubital veins as strong as other nearby veins ..... **Colletidae-COLLETINAE** (p. 995)

**65. Colletidae.** This family is better represented in Australia than in any other region. Its members range from large, robust, hairy bees to some of the smallest, most slender and barest in the world. They are usually readily recognisable by the short broad glossa which may be truncate, emarginate or bifid (Fig. 42.43A; in males of a few Hylaeinae it is acute apically).

Colletidae are unique among bees in that they line their brood cells (and sometimes other parts of the nest) with a colourless, cellophane-like material. This is a polyester formed from a liquid apparently secreted by the abdominal Dufour's gland (or thoracic salivary gland in Hylaeinae) and applied by the brush-like glossa of the female (Batra 1980). As far as known, all members of the family are solitary and none is parasitic except perhaps a few Hawaiian species. Two subfamilies not represented in Australia are the Western Hemisphere Diphaglossinae and Xeromelissinae (= Chilicolinae).

Several Australian species have either the labial or maxillary palps enlarged (in some cases extraordinarily elongated) as an aid for collecting nectar from flowers with deeply recessed nectaries (Houston 1983a).

#### Key to the Subfamilies of Colletidae Known in Australia

1. Fore wing with 3 submarginal cells or, if with 2, 2nd about as long as 1st; scopa present in ♀♀ (consisting of abundant, plumose setae on hind legs); pygidial plate present in ♀♀, broadest basally (except in *Callomelitta*); basitibial plate usually present and defined by a carina; relatively hairy bees ..... **COLLETINAE**

Fore wing with 1 or usually 2 submarginal cells, 2nd usually much shorter than 1st; scopa absent; pygidial plate, if present, usually narrow and parallel-sided or spoon-shaped (Fig. 42.44C); basitibial plate usually absent or incompletely defined; relatively bare or short-haired bees ..... 2

- 2(1). Pygidial plate of ♀♀ present, slender and more or less parallel-sided (Fig. 42.44C); basitibial plate usually recognisable although often demarcated only by a few tubercles or only the apex indicated by a tubercle; anterior tentorial pits located well above middle of lateral margins of clypeus (Fig. 42.44G) ..... **EURYGLOSSINAE**

Pygidial plate absent or, in the few species that possess it, not as above; basitibial plate usually absent, rarely weakly defined apically; anterior tentorial pits located at or below middle of lateral margins of clypeus (Fig. 42.44F) ..... **HYLAEINAE**

The world-wide **COLLETINAE** (Fig. 42.45D) are moderate-sized, hairy bees which (with one known exception in *Leioproctus*) transport pollen externally on scopal hairs of the hind legs. The only Australian tribe is the very large **Paracolletini**. These nest in the ground or occasionally in rotting wood. Each ovoidal cell is at the end of a lateral burrow radiating from the shaft. Provisions vary from moulded, subspherical balls of pollen to liquid mixtures of pollen and honey. Included genera are *Callomelitta*, *Hesperocolletes*, *Leioproctus*, *Neopasiphae*, *Paracolletes* and *Trichocolletes*.

The endemic **EURYGLOSSINAE** (Figs 42.44C, G, 45C) are

moderate-sized to minute bees, usually sparsely hairy and often with pale markings (many are partially or wholly yellow or white). As in Hylaeinae, there is no scopa of pollen-carrying hairs and pollen is transported to the nest in the crop. Most species nest in the ground but some nest in dead wood. The nests are usually much like those of the Paracolletini but the cells are sometimes constructed in linear series and the provision is always a viscid, liquid mixture of pollen and honey (Houston 1969). Included genera are *Euryglossa*, *Euryglossina*, *Pachyprosopis* and several less well known groups. [Exley 1968–83]

The world-wide HYLAEINAE (Figs 42.44F, 45A) are also moderate-sized to minute, sparsely hairy bees, usually dark with yellow or white marks on the face and thorax. As in Euryglossinae there is no scopa and pollen is carried to the nest in the crop. Nests usually are constructed in burrows in pithy stems or holes made by beetle larvae or other borers in woody stems or in logs and stumps. Some species nest in the ground. The cells resemble tiny, cellophane packets and are constructed end to end in the burrow, sometimes with wads of pith or wood fibre,

or secreted partitions between them. The provision is a liquid, pollen-honey mixture. Several young adults of some species may be present in a single nest before they disperse to establish new ones, and one female may even begin provisioning cells while her sisters are still in the nest. Males of some genera have the glossa pointed, unlike any other Colletidae. Australian genera are *Amphylaeus*, *Heterapoides*, *Hylaeus* (Fig. 42.45A), *Hyleoides* (Plate 6, G), *Meroglossa*, *Palaeorhiza* and several less common genera. [Houston 1975b, 1981]

**66. Stenotritidae** (Figs 42.44E, 45E). Large, densely pubescent bees (body length 14–20 mm). Prior to 1980, this endemic Australian group was treated as a subfamily of Colletidae. The mouth-parts are colletid-like except that the glossa is rounded-acute apically rather than truncate or emarginate. Other distinguishing features are the low-set ocelli, paired subantennal sutures, elongated 1st flagellar segment (longer than scape) (Fig. 42.44E), absence of the pre-episternal groove and vestigial sting. The compound eyes of males are often strongly convergent dorsally. The only genera, *Stenotritus* (ca 20 spp.)

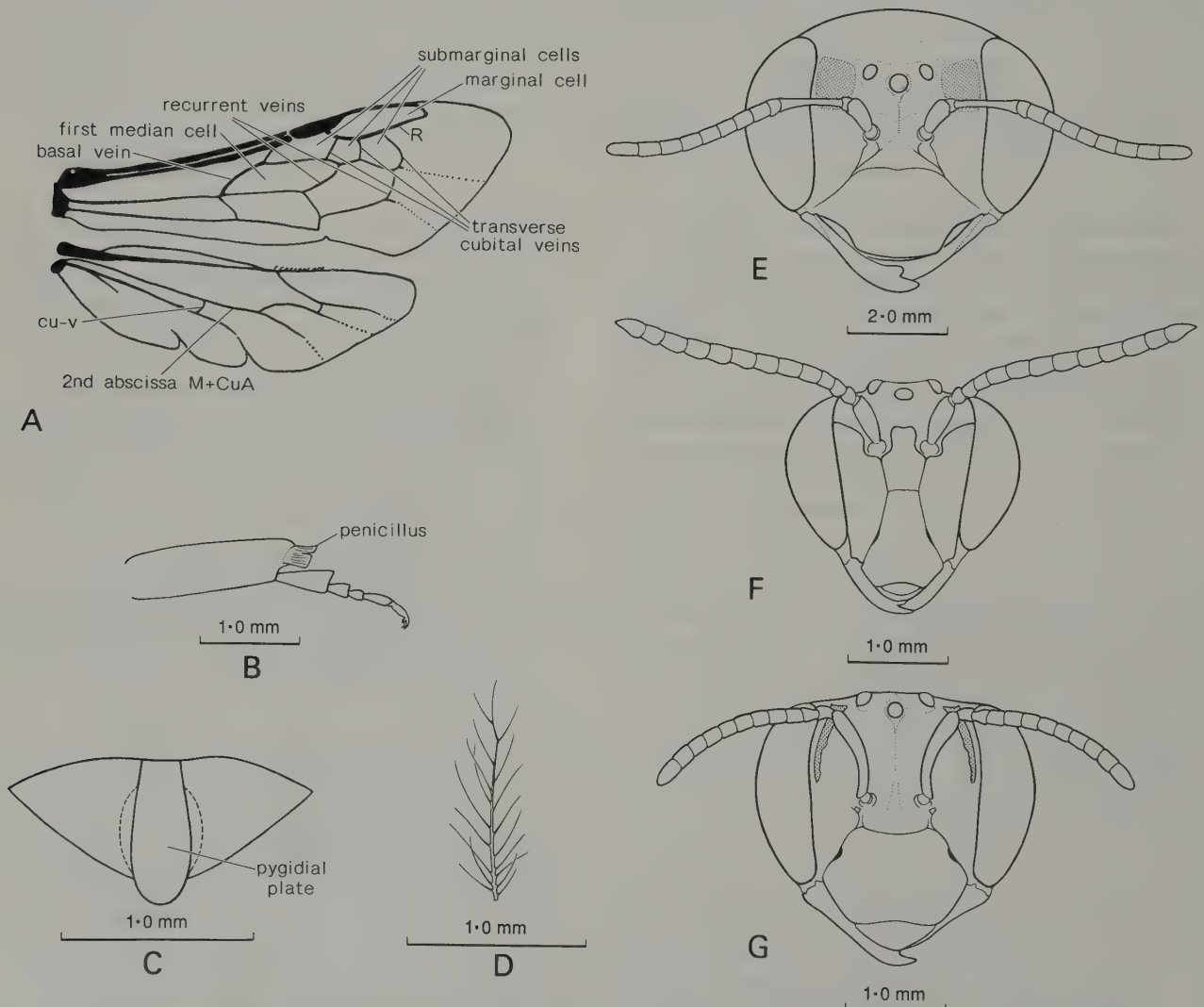


Fig. 42.44 Apoidea: A, wings of a colletid, showing veins and cells referred to in the key; B, hind tarsus of ♀ halictid; C, T6 of ♀ euryglossine; D, branched hair; E, head of ♀ stenotritid, frontal; F, head of ♂ hylaeine, frontal; G, head of ♀ euryglossine, frontal.

[A. Hastings]





Fig. 42.45 Apoidea, ♀♀: A, *Hylaeus elegans*, Colletidae-Hylaeinae; B, *Trigona essingtoni*, Apidae-Meliponinae; C, *Euryglossa depressa*, Colletidae-Euryglossinae; D, *Leioproctus megachalcoides*, Colletidae-Colletinae; E, *Ctenocolletes smaragdinus*, Stenotritidae; F, *Nomia australica*, Halictidae-Nomiinae; G, *Megachile chrysopyga*, Megachilidae-Megachilinae; H, *Thyreus nitidulus*, Anthophoridae-Anthophorinae; I, *Exoneura bicolor*, Anthophoridae-Xylocopinae; J, *Amegilla cingulata*, Anthophoridae-Anthophorinae.  
[A–C, F–J by M. Quick; D, E by A. Hastings]

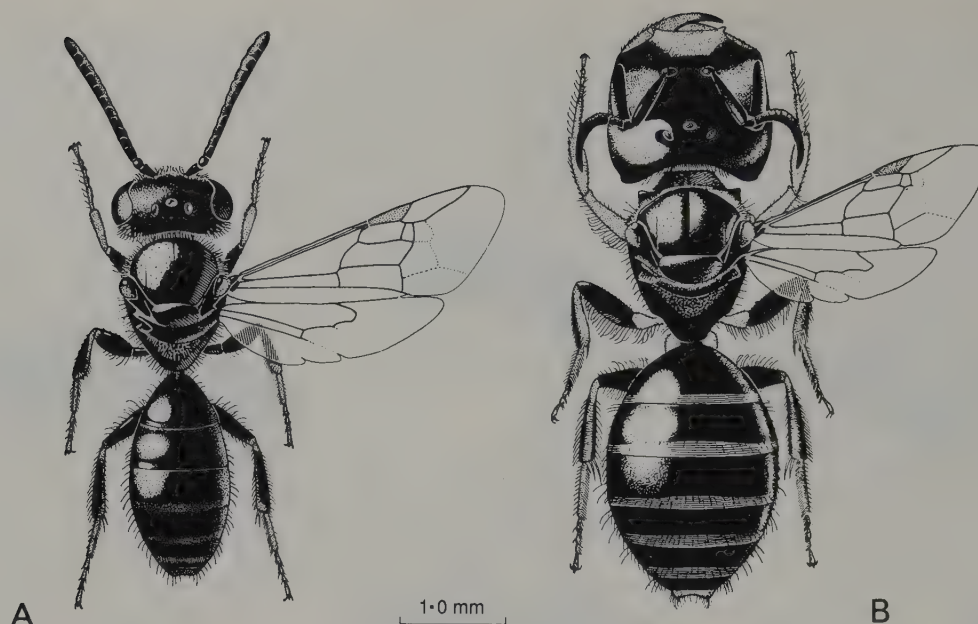


Fig. 42.46 Male polymorphism in *Lasioglossum* sp., Halictidae: A, normal ♂; B, large, flightless ♂.

[From Houston 1970]

and *Ctenocolletes* (10 spp.), are best represented in W.A. and only the former occurs in the eastern states (except Tas.). [Houston 1983b,c, 1985]

Stenotritids are solitary ground-nesters. Single, cemented, earthen brood cells are constructed at the ends of lateral burrows extending from the end of a shaft. The larval provision is a moulded mass of moist pollen. Various aspects of the biology are dealt with by Houston (1975a, 1984b, 1987) and Houston and Thorp (1984).

**67. Halictidae** (Figs 42.44B, 45F, 46). A large cosmopolitan family of minute to moderate-sized bees, usually black, often at least partly metallic green or blue, and frequently with their abdomen orange-brown. Pubescence is moderately abundant (except in the parasitic *Sphecodes*) and usually forms a pollen-carrying scopa on the hind leg from coxa to basitarsus and sometimes also on adjacent parts of the body. However, in *Homalictus* the scopa is chiefly confined to the underside of the metasoma.

#### Key to the Subfamilies of Halictidae Known in Australia

- 1st and 3rd submarginal cells subequal in length (Fig. 42.45F), contrasting with much shorter 2nd submarginal cell; pre-episternal groove absent or inconspicuous below scrobal groove; T6 of female with undivided band of pubescence ..... NOMIINAE
- 1st and 3rd submarginal cells markedly unequal, 3rd much shorter, often not much longer than 2nd (Fig. 42.46A); pre-episternal groove continuing below scrobal groove; T6 of female with band of pubescence divided medially ..... HALICTINAE

The HALICTINAE include the Australian genera *Homalictus*, *Lasioglossum* and *Nomioides*. The first two are in the tribe Halictini, the third is in the tribe Nomiodini; the remaining tribe, Augochlorini, is New

World. The nest burrows, usually in the ground but occasionally in rotting wood, are often branched and lead to cells which are either at the ends of lateral burrows or clustered near branch or main burrows. Cell clusters commonly are surrounded by cavities. Cells in Australian genera are more or less horizontal and are lined by a thin layer of waterproofing secretion. The egg is laid on top of a firm, moulded subspherical mass of moist pollen which rests on the lower flatter side of the cell. Australian species may be solitary or communal (from 2 to more than 100 females may share a nest; each is fertilised and lays eggs in cells of her own making). Eusocial colonies, with workers and one or a few queens, are known from other continents, but not from Australia. An unusual polymorphism occurs in males of some communal species (Fig. 42.46). Large-headed, small-winged males occur along with normal males but are restricted to the nests. Macrocephalic males fight one another for possession of the nest and its females and also repel intruding parasites. There are several parasitic genera elsewhere in the world and two species of *Sphecodes*, presumably parasitic in nests of other halictids, reach northern Australia. Nesting biology of Australian halictines is discussed by Knerer and Schwarz (1978). [K. L. Walker 1986; Yeates and Exley 1986]

The NOMIINAE, containing the one genus *Nomia* (Fig. 42.45F), make nests similar to halictines except that the cells are vertical and the provision mass is much more highly compressed, sometimes rather disc-shaped, and rests across the lumen of the cell.

**68. Ctenoplectridae.** This small family of two genera is characterised by having mouth-parts essentially like those of long-tongued bees except that the labial palps are short and unmodified as in short-tongued bees. There are only 2 submarginal cells, the distal half of the marginal



cell gradually curves away from the wing margin, and females have a large, crescentic, inner hind tibial spur with a comb-like array of long, fine teeth on the concave margin. *Ctenoplectra australica* from northern Qld is the only Australian representative. Related species are known to collect oil from flowers of Cucurbitaceae, to nest in pre-formed cavities (usually in wood) and to construct cells from soil transported to the nest site (Michener and Greenberg 1980).

**69. Megachilidae** (Fig. 42.45G). This world-wide family of small to very large, long-tongued bees is one of the most readily recognised in Australia. The large head is usually well developed in the genal and occipital regions. There are always 2 submarginal cells, with the 2nd as long, or nearly as long, as the 1st. The scopa (absent in *Coelioxys*) is on the abdominal sterna, not the legs.

Most Australian megachilids belong to the MEGACHILINAE in which there are no pygidial or basitibial plates and the jugal lobe of the hind wing is short. *Chalicodoma*, *Coelioxys* and *Megachile* (Fig. 42.45G) belong to the Megachilini, and *Anthidiellum*, restricted in Australia to the north and distinguished by having yellow integumental margins, belongs to the Anthidiini. LITHURGINAE, containing only *Lithurge*, are distinguished by certain primitive characteristics such as a long jugal lobe on the hind wing and remnants of a pygidial plate. Fideliinae (formerly Fideliidae) are not known from Australia.

No members of this family are social. Some are parasitic in the nests of other megachilids (in Australia, *Coelioxys* inhabits the nests of *Megachile*). Although some megachilids (especially *Lithurge*) excavate new burrows, most use pre-existing burrows or hollows and a few (*Anthidiellum* and some *Chalicodoma*) build exposed nests on rocks or plants. Megachilinae are noteworthy for their use of foreign materials carried to the nests from other locations. *Megachile* makes its nests of neatly cut pieces of leaves (commonly rose leaves). *Chalicodoma* uses resin and/or masticated leaves and may incorporate soil, pebbles and other materials. *Lithurge* excavates branching burrows in dead wood and the cells in the blind ends of burrows are plugged with barricades of wood frass. Larval provisions of megachilids vary from a thick paste to a firm mass of pollen filling the distal part of the cell and the egg is deposited on the free surface (except in *Lithurge* which deposits it within or beneath the provisions (Houston 1971)). Mature larvae spin strong cocoons (not usually found in short-tongued bees).

**70. Anthophoridae** (Figs 42.43B, D, 45H-J). Small and bare to large and densely pubescent, long-tongued bees. The pollen-carrying scopa (absent in parasitic forms) is restricted to the hind tibiae and basitarsi. This large, diverse and cosmopolitan family is poorly represented in Australia by three subfamilies which differ greatly from one another in behaviour.

*Key to the Subfamilies of Anthophoridae Known in Australia*

1. Pygidial plate absent or represented by apical spine usually hidden in dense pubescence; clypeus not

strongly protuberant, lateral parts seen from below but little bent back and not parallel to long axis of body ..... XYLOCOPINAE

Pygidial plate present in ♀; clypeus strongly protuberant, so that, seen from below, lateral parts are bent back parallel to long axis of body ..... 2

- 2(1). Marginal cell longer than distance from its apex to wing tip, pointed on wing margin; pterostigma large, extending well into marginal cell beyond base of vein R ..... NOMADINAE

Marginal cell shorter than distance from its apex to wing tip, apex of cell rounded and separated from wing margin; pterostigma small, not extending into marginal cell beyond base of vein R (Figs 42.45H, J)

..... ANTHOPHORINAE

Numerous tribes of NOMADINAE occur on other continents. Only Nomadini reach Australia, represented by *Nomada* in Qld. All Nomadinae are cleptoparasitic and lack a scopa. Australian species are rather small, slender, wasp-like insects with short, sparse pubescence and presumably cleptoparasitise halictids or other ground-nesting bees.

Two of the several tribes of ANTHOPHORINAE reach Australia. Anthophorini (Fig. 42.45J) are represented by the large, robust, hairy, often banded bees of the genus *Amegilla*. They often nest in aggregations, either in flat ground or in banks of soil, but each female makes her own burrow and cells. Each cell is lined with a layer of secreted, wax-like material and the provisions are liquid or semi-liquid. Larvae do not spin cocoons. The Melectini (Fig. 42.45H) contain *Thyreus*, robust bees without much long hair but adorned with striking white or blue patches of appressed hairs. They are cleptoparasitic in the nests of *Amegilla*.

The XYLOCOPINAE (carpenter bees) include three very different looking tribes. Xylocopini, represented by *Xylocopa* and *Lestis* (Plate 5, U), are large to very large, robust, hairy bees, black or metallic green, and often with yellowish pubescence. They excavate burrows in dead branches of trees or in dead pithy flower stalks of *Xanthorrhoea*. The cells are built end to end in these burrows, are unlined, and each is provisioned with a firm mass of pollen on which the egg is laid. Ceratinini are small, largely bare, black or usually greenish bees, with white or cream marks on the face and with 3 submarginal cells. *Ceratina* is represented in Australia by only one species. It nests in pithy stems and constructs series of cells basically similar to those of the Xylocopini. Allodapini resemble Ceratinini but have 2 submarginal cells and the abdomen is black or orange-brown. *Braunsapis* and *Exoneura* (Fig. 42.45I) also nest in pithy stems or in burrows made by other insects in wood. These two genera and other allodapine bees are unique in that they do not construct brood cells, the larvae being reared together and fed progressively in the nest burrow. The larvae thus occupy an environment very different from that of most bee larvae, and have head and body projections unlike those of other bees.

In at least some Allodapini there is a primitive social organisation, nests being occupied by two or more

females which may differ with respect to whether or not they mate, lay eggs and forage. The nature of the social organisation has not been fully studied but it may differ from species to species and among nests of the same species. Females in nests may be of the same or different generations (i.e. all sisters, or mothers and daughters). Egg-layers may be sedentary and larger than their infertile foraging nest-mates or active and morphologically undifferentiated (Michener 1965a; Houston 1977; Schwarz 1986).

*Inquilina* is closely related to *Exoneura*. It differs primarily by the reduction of the scopa, and lives as a social parasite in the nests of some *Exoneura*. There are also species of *Braunsapis* which appear to be social parasites in the nests of other species of their genus (Michener 1961a).

**71. Apidae** (Fig. 42.45B). A world-wide family of long-tongued bees in which pollen is carried in corbiculae. It includes all the highly social bees and the Neotropical Euglossinae, most of which are solitary or at most communal. The Bombinae, not represented in Australia, include the bumble bees (*Bombus*) and the Euglossinae. Efforts to establish European species of *Bombus* in Australia have been unsuccessful although several are established in New Zealand. APINAE are represented by the introduced honey bee, *Apis mellifera*, and MELIPONINAE by native species of *Trigona*.

*A. mellifera* is of commercial importance as a honey producer and pollinator in many parts of the continent. It visits a wide range of native flowers and feral colonies nest in hollow trees, holes in banks and cliffs and other sites. The combs of cells are made of secreted wax and are vertical, suspended from some support in the nesting cavity. Honey and pollen are stored in cells similar to brood cells. The female castes differ from one another, the queen lacking corbiculae and being unable to survive without accompanying workers. *A. mellifera* is easily distinguishable from almost all other Australian bees by its densely hairy eyes. It is the only bee in Australia that leaves its sting in a victim.

*Trigona* (Fig. 42.45B) includes the small dark 'native honey bees', 'stingless bees' or 'sugar bag bees' of northern and eastern Australia. Like honey bees, they exist in large colonies consisting of a structurally strikingly differentiated queen without corbiculae, and thousands of workers. Unlike honey bees, they are unable to sting. Instead, they may crawl over an intruder and bite. The nests, composed of cerumen (a mixture of resin and secreted wax), are usually built in tree hollows and sometimes in rock crevices. Brood cells are arranged in clusters (Australian species of the subgenus *Plebeia*) or in



Fig. 42.47 Workers of *Oecophylla smaragdina*, Formicidae, drawing together leaves which are bound with silk from larva held by worker on right: ants 8 mm long (reconstructed from photos by A. J. Nicholson and R. W. Taylor).  
[F. Nanninga]

horizontal combs with the cells opening upwards (subgenus *Tetragona*), unlike the vertical combs of *Apis*. Honey and pollen are stored in large wax pots quite unlike the brood cells. Layers of cerumen may surround the whole nest and the brood cells. Establishment of new nests is not by the departure of the old queen and a swarm of workers as in *Apis*, but is a gradual process in which workers from a nest locate a new site, carry nesting materials there, construct a new nest, and even carry provisions to it. Ultimately, a young queen goes there and establishes herself with a group of workers, but interchange between the new and old nest may go on for some weeks after the arrival of the young queen at the new nest. Old queens are so swollen and heavy that they cannot fly, and hence cannot depart to establish new nests as in *Apis*. In *Trigona*, queens are produced in special large queen cells, as in *Apis*. Nests of Australian species have been described by Michener (1961b).

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This is not a bibliography: it merely provides an entry into main literature. Musgrave (1932) published a bibliography of Australian entomology to 1930, and copies of his second, unpublished (uncorrected) volume, covering the period 1931–58, are held by the Australian Museum, Sydney, the Australian Academy of Science, Canberra, and the Division of Entomology, CSIRO, Canberra. World literature from 1864 is covered by the *Zoological Record*, issued annually. In the following list, abbreviations are, where possible, those given in the 4th edition of *The World List of Scientific Periodicals* (London: Butterworths, 1963–65), and the numbers in square brackets are the chapters in which the references are cited.

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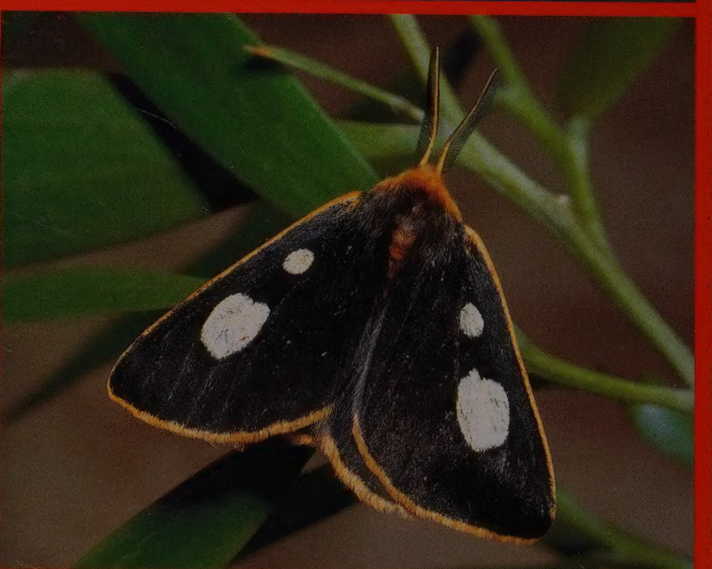
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